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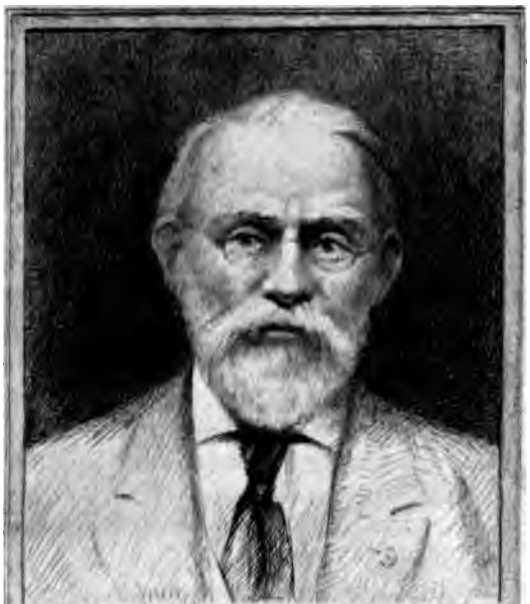

THE SCIENTIFIC MEMOIRS

OF

THOMAS HENRY HUXLEY

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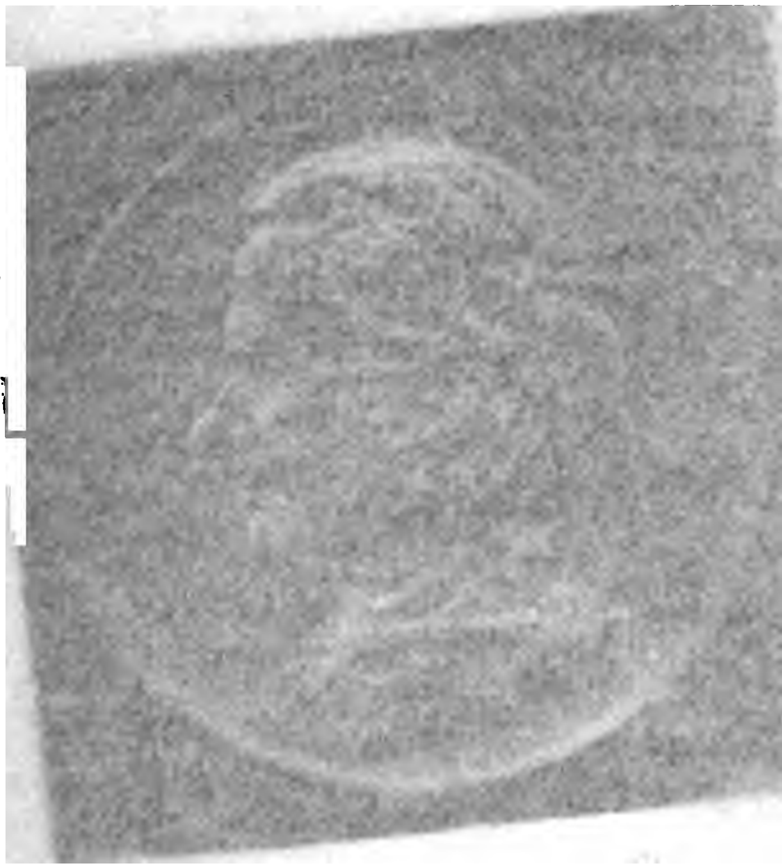

THE SCIENTIFIC MEMOIRS

OF

THOMAS HENRY HUXLEY

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THE SCIENTIFIC PAPERS OF THOMAS HENRY HUXLEY

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ON THE STRUCTURE OF THE SKULL AND OF THE HEART OF *MENOBRANCHUS LATERALIS.*

Proceedings of the Scientific Meetings of the Zoological Society of London, 1874, *pp.* 186–204. (*Read March* 17*th*, 1874.)

(PLATES XXIX.—XXXII. [PLATES 1—4]).

1. *The Skull.*

IN 1835, Mayer, in his "Analecten für vergleichende Anatomie," published a brief account of the anatomy of *Menobranchus lateralis.* Under the head of "Osteologie" (p. 82), he remarks:—

"The skull has a singular form, which results from the brevity of the mandible and the direction of the long quadrate bone obliquely forwards and downwards." "As in *Menopoma*, the rami of the mandible are not ankylosed together, though the three pieces of each ramus are more closely united than in *Menopoma.* In the skull are distinguishable:—the articular portions of the occipital bone (*b*), which, below, appear not to be separate from the sphenoid (Keilbein) and vomer; above, however, they do not extend to the top of the skull. The parieto-temporal bones (Scheitelschläfenbeine) (*c′*), which are broad and arched, forming laterally the roof of the vestibule. The frontal bones (*c*). The long and bent quadrate bones (*n*). The pterygoid bones (*m*), with their teeth. Between them the great opening for the fifth pair (*x*)." "The nasal bones are wanting. The maxillæ (*k*) and the præmaxillæ (*f*)." A fair figure (tab. vii. fig. 2)

accompanies this short notice, from which it is clear that Mayer's "maxillæ" are the vomers, and his "quadrate" the squamosal.

A short description of a skull of *Menobranchus* in the Museum of the Royal College of Surgeons is to be found in the first volume of the "Catalogue of the Osteological Series," p. 116. The prominent ossification of the epiotic bears the number appropriated to the "mastoid" by Professor Owen. Fischer ("Anatomische Abhandlungen über die Perennibranchiaten und Derotremen," 1864) has given an excellent description and figure of the hyoidean and branchial arches of *Menobranchus*. The fullest account, and the best figure, of the skull of *Menobranchus* which I have met with, however, are contained in Van der Hoeven's "Ontleed-en Dierkundige Bijdragen tot de Kennis van *Menobranchus*," published in 1867. Van der Hoeven distinguishes the following bones:—the lateral occipitals (exoccipitals *mihi*), the *os sphenoideum* (parasphenoid), the *os pterygoideum* (pterygopalatine), the *os petrosum* (epiotic and opisthotic), the *os parietali-frontale* (parietal), the *os frontale anterius* (frontal), the *os frontale posterius* (prootic), the vomers, the *os tympanicum* (squamosal), and the *os jugale* (quadrato-jugal); in the mandible, the *os dentale* (dentary), and the *os angulare* (splenial).

In his description of the hyoidean and branchial arches, Van der Hoeven agrees with Fischer. As to the manner in which the hyoid is connected with the suspensorium, the latter writer observes that the ascending branch of the hyoidean cornu is connected by ligament with the posterior surface of the "os tympanicum." "In *Hypochthon* a second strong ligament extends from the dorsal apex of the hyoidean cornu to the lower jaw. In none of the other genera [of Perennibranchiata and Derotremata] have I observed this second attachment to the lower jaw. A tendon, which, in *Menobranchus*, runs external to the posterior point of the hyoidean cornu, parallel with the latter, downwards and forwards, belongs to the second portion of the digastric muscle." Nevertheless it will be seen that this second ligament exists no less in *Menobranchus* than in *Proteus*. It is also to be found in *Siren* and *Siredon*. None of the authors cited mentions the cartilaginous framework of the skull.[1]

The cranium of *Menobranchus* viewed from above (Plate XXX. [Plate 2], fig. 1), presents the form of a pentagon, with a deeply

[1] Stannius observes ('Handbuch. die Amphibien,' p. 38), "Bei den *Proteidea* [*Proteus* and *Menobranchus*] sind die niedrigen Seitenwände der beiden vordersten Segmente de eigentlichen Schedelcapsel nicht ossificirt," and that they have an abortive cartilagino antorbital process. He also mentions that the ligament which extends from the præmax to the suspensorium contains particles of cartilage (eingesprengte Knorpel). I have noticed these in my specimen.

excavated base, and with the angle opposite the base truncated. This truncated angle corresponds with the ends of the premaxillary bones ; the lateral angles are occupied by the extremities of the suspensoria, or peduncles to which the mandible is attached ; the posterior angles answer to the epiotic processes of the skull of an osseous fish. As these project beyond the level of the occipital foramen, they give rise to the excavated contour of the base of the pentagon. The occipital condyles lie one on each side of and below the occipital foramen ; and their slightly convex free surfaces look inwards and backwards. In a side view (Plate XXIX. [Plate 1], fig. 1), the skull is seen to be much flattened from above downwards. The suspensorium is inclined downwards and forwards at an acute angle with the cranio-facial axis. The ramus of the mandible is proportionally stout and thick, and the hyobranchial apparatus, though almost wholly cartilaginous, is massive and large relatively to the skull.

The skull consists of a cartilaginous framework, in and upon which certain ossifications have been developed. The former is what is commonly termed the " primordial cranium ; " but, as it is preceded by a membranous structure, it would be better termed the "chondrocranium," while the bony skull may be called the "osteocranium."

The *osteocranium* consists of the following bones :—

1. The *exoccipitals* (*E.O*).—These lie on each side of the occipital foramen, and bear the condyles. They do not come into contact either above or below; but the small space left between them is covered by the parietal bones in the former region, and by the parasphenoid in the latter.

2. The *epiotics* (*Ep.O*).—I term these interesting ossifications " epiotic " for brevity's sake. In reality they represent not only the epiotic but the opisthotic ossifications of other Vertebrata. They are conical caps of bone, which are separated by narrow cartilaginous interspaces from the pro-otics (*Pr.O*) in front, but closely unite with the exoccipitals behind and below. As usual, they shelter the posterior part of the organ of hearing; and the *fenestra ovalis*, with its stapes (*St*), is situated in the unossified interspace between the anterior and inferior (or opisthotic) part of the bone and the pro-otic.

3. The *pro-otic* ossifications (*Pr.O*) occupy their ordinary place in the front part of the capsule of the organ of hearing, and are covered above by the parietals (*Pa*), and externally by the squamosals (*Sq*).

4. The *parasphenoid* (*P.Sph*) is a very wide and thin bone, which

extends from the lower margin of the occipital foramen, posteriorly, to a point beyond the middle of the length of the vomers, anteriorly. It underlies the exoccipitals, the epiotics, and the pro-otics behind, while, in front, the vomers underlie it on each side. Its anterior extremity is truncated, and slightly concave forwards.

5. The *vomers* (*Vo*) are much elongated, flattened, broader behind than in front, and have a sigmoid curvature, which is especially manifested by their inner edges. As the vomers come into contact only by their anterior extremities, while their inner edges diverge from one another backwards, there is left between them a wide space, increasing in breadth posteriorly, which is occupied, for the greater part of its extent, by the parasphenoid, but, in front of the truncated anterior termination of this bone, by a part of the chondrocranium. A series of teeth is set along the outer edge of each vomer; and its posterior excavated extremity articulates with the palatine bone.

6. The *parietal* bones (*Pa*), which are broad and flat, cover over the greater part of the epiotic and pro-otic bones. They meet in a median sagittal suture, which is about half as long as the whole skull. Anteriorly, each parietal bone presents three processes. The innermost of these (Pa^1) is the proper continuation of the bone; uniting with its fellow, it gives rise to the anterior half of the sagittal suture, and extends forwards, as a long triangular tongue, which is interposed between the two frontals (*Fr*). The second (Pa^2) and third (Pa^3) processes start from a common root. The inner, very long and slender, runs along the outer edge of the frontal bone, widening a little as it goes, and ends at the posterior boundary of the olfactory foramen (I). The third process (Pa^3) is short, passes downwards and outwards, and rests, in a manner to be described presently, upon a cartilage connected with the suspensorium.[1]

7. The *frontal bones* (*Fr*), separated behind by the conjoined parietals, unite, in front, in a long frontal suture, and terminate, anteriorly, in pointed processes, which are received between the ascending processes of the premaxillary bones. Between the latter and the olfactory foramen, each frontal is continued into a plate of bone (Fr^1), which lies on the sides of the snout. The anterior, pointed extremity of this plate fits in between the ascending process of the premaxilla and the vomer, while its posterior prolongation passes below the olfactory aperture, to the cartilaginous antorbital process of the skull.

[1] Professor Owen considers that this process represents "the so-called columella of Lizards" (*l. c.*, p. 116.)

8. A *quadrate* ossification (*Qu*), of irregular form, occupies the distal end of the cartilaginous suspensorium.

9. The *palato-pterygoid* (*Pl Pt*) is a flattened plate of bone, rounded and spatulate in front, where it articulates with the excavated posterior end of the vomer ; truncated behind, where it underlies the suspensorium.

10. The *præmaxillæ* (*Pmx*). These are relatively strong bones, each composed of a horizontal "body" bounding the gape in front, and of a strong ascending process, which passes back on to the top of the skull, at an acute angle with the body of the bone. The "body" tapers off to a point posteriorly; and, in the specimen the skull of which I examined, there was no maxilla whatever, mere fibrous tissue connecting the end of the præmaxilla with the outer extremity of the antorbital process, and bounding the posterior nasal aperture externally. But in the skeleton of *Menobranchus* prepared by Hyrtl, now in the Museum of the Royal College of Surgeons, there is, on the right side, a minute bone bearing three teeth, which seems to be a rudimentary maxilla.

11. The *squamosals* (*Sq*) are long slender bones, which extend from near the extremity of the epiotic processes to the articular surface for the mandible on the extremity of the suspensorium. The whole bone is shaped somewhat like a boomerang—the half which lies against the outer side of the suspensorium being bent at an obtuse angle to the half which is connected with the pro-otic, parietal, and epiotic bones, and which runs parallel with the axis of the skull. Where the cranial and suspensorial portions of the bone meet, there is given off, from its posterior margin, a short osseous process, which is directed towards the stapes, covering over the ligamentous fibres which connect the stapes with the suspensorium.

12. The *dentary* (*D*) occupies the whole length of the mandible, rising up on its outer side into a high plate, curving inwards to the symphysis in the middle line, and extending as a shelf, grooved above, beneath Meckel's cartilage, which is received into the groove. Fourteen conical teeth are borne by this bone, and are ankylosed with it.

13. The *splenial* (*Spl*, Plate XXXI. [Plate 3], fig. 7) lies on the inner side of Meckel's cartilage, and bears six teeth.

14. The only other ossified member of the cranial, or facial, series present in *Menobranchus* is the second basibranchial (Bb^2, Plate XXX, [Plate 2], fig. 2), a styliform bone, broader in front than behind, which lies in the middle line, and articulates, in front, with the two anterior cerato-branchials (Cb^1).

The *chondrocranium*, in and upon which the bones now enumerated and described are developed, is a structure of an exceedingly remarkable character. The whole extent of the chondrocranium was ascertained by decalcifying the skull, macerating it afterwards in glycerine containing caustic potash, and then, partly, viewing it as a transparent object, and, partly, examining sections.

In the side walls of the depressed cranial cavity, between the parasphenoid and the second process of the parietal bone (Pa^2), there lies a rod of cartilage, which, at the anterior boundary of the orbit, is connected with the tapering antorbital process (*A.O*). It then bends inwards (on the inner side of the olfactory sac); and, meeting its fellow in the middle line, the two proceed, parallel with one another, to the end of the snout, their free extremities being embraced by the præmaxillæ.

The antorbital process is separated from the chief mass of this rod, which corresponds with one of the *trabeculæ* of the ordinary embryonic vertebrate cranium, by a line of fibrous tissue. In the internasal region, on the other hand, the anterior ends of the cartilaginous rods (which answer to the cornua of the trabeculæ) become fused together.

Posteriorly, each trabecula passes into the floor of a cartilaginous mass, which is formed, above, by the auditory capsule, and, behind, by the exoccipital, and which has undergone partial ossification. But, in spite of careful search, I could find no cartilage either in the supraoccipital, or in the basioccipital, region, but only a dense connective tissue. In the midst of this, in the basioccipital region, the conical extremity of the notochord is imbedded.

The large oval space included between the trabeculæ, their subauditory continuations, and the inferior and internal edges of the exoccipitals, is floored by fibrous tissue, in which the parasphenoid is developed, just as the roof of the skull is constituted by the fibrous tissue in which the parietals and frontals are formed. The side walls of the cranial cavity are constituted, behind, by the exoccipitals and auditory capsules, in front of these, by the trabeculæ: and, external to them, by the second processes (Pa^2) of the parietal bones.

The suspensorial cartilage presents, anteriorly and below, an oval, concave, articular facet for the articular end of Meckel's cartilage. Just above this, on the inner side, is a small elevation (*p*, Plate XXXI. [Plate 3], fig. 4), which is all that represents the palatopterygoid process of other *Amphibia*. Still higher up, on the inner side, the suspensorium gives off a broad, tongue-shaped, "ascending-

process" (*a*, Plate XXX. [Plate 2], fig. 1), which mounts beneath the "third process" of the parietal bone, and applies itself to the outer side of the trabecular cartilage. The orbito-nasal (ophthalmic) division of the trigeminal nerve (V^1) passes beneath this tongue of cartilage, which therefore, morphologically speaking, ascends higher than the eye, inasmuch as the orbito-nasal nerve, as it passes forwards, runs above the optic nerve (Plate XXIX. [Plate 1], fig. 1 and Plate XXXI. [Plate 3], fig. 4).

The orbito-nasal nerve actually leaves the skull by a considerable foramen, common to it and the other divisions of the fifth ($V^{2,3}$), which lies between the trabecula internally and below, the pro-otic externally and behind, and the parietal bone above. And this foramen is undivided; but, as the ascending process of the suspensorium passes between the orbito-nasal nerve on its inner and anterior side, and the second and third divisions of the fifth on its outer and posterior side, it looks as if the process in question divided the foramen of exit of the trigeminal nerve into two parts.

The ganglia of the trigeminal and of the seventh nerves are situated, close together, above the trabecula, where it passes into the floor of the auditory capsule—the Gasserian ganglion lying in front of the anterior wall of the capsule, while the ganglion of the seventh, which is very closely connected with the auditory nerve, is placed rather on the ventral side of the anterior end of the capsule (Plate XXXI. [Plate 3], fig. 4). Immediately in front of these ganglia, the trabecula is produced externally, and becomes continuous with the suspensorium by the process (*m*), which thus affords the middle and chief attachment of the suspensorium to the skull, and may be named the "pedicle of the suspensorium." Finally, the external and posterior angle of the suspensorial cartilage is produced upwards and backwards, on the exterior of the auditory capsule, with which it is closely adherent, into an *otic* process (*o*, Plate XXXI. [Plate 3], fig. 4). The posterior division of the seventh nerve (which answers to what is commonly called the facial nerve, and may be termed the *hyo-mandibular* division of the seventh) runs directly in front of the auditory capsule, and beneath the otic process of the suspensorium. The anterior division (palatine or Vidian division), of the seventh, on the contrary, passes directly forwards, close to the pedicle of the suspensorium, parallel with the orbito-nasal, and below but external to it.

Meckel's cartilage (*Mck*) is very thick at its articular end, but rapidly tapers off to a point beyond the coronoid enlargement, to which the elevators of the jaw are attached. The termination of

Meckel's cartilage lies at a considerable distance from the symphysial end of the ramus of the mandible (Plate XXIX. [Plate 1], fig. 1. and Plate XXXI. [Ptate 3], fig. 7).

The hyoidean arch has already been well described and figured by Fischer. It is entirely cartilaginous and fibrous. It consists (Plate XXX. [Plate 2], fig. 2), of a long and stout *ceratohyal* cartilage (*C.h*), and a small *hypohyal* (*H.h*). The two *hypohyals* are united with one another by fibrous tissue, which represents the *basihyal*. Fibrous tissue connects the proximal half of the ceratohyal with the suspensorium and with the otic region of the skull ; and a strong ligamentous band, the *hyo-suspensorial* ligament (*h.s.l.*), Plate XXIX. [Plate 1], fig. 1), passes from the ceratohyal, at about the junction of its middle and upper thirds, to the middle of the posterior edge of the suspensorium. From this point another strong fibrous bundle, the *suspensorio-stapedial* ligament (*s.s.l.*), is continued upwards and backwards to the stapes. The hyo-mandibular branch of the seventh nerve (VII.*p.*) passes above this ligament to its distribution, just as it passes above the *columella auris* in the Frog.

Rather above the attachment of the hyo-suspensorial ligament, another strong band of fibrous tissue arises from the ceratohyal, and, passing down on the inner side of the former, is inserted into the angle of the mandible. This may be termed the *mandibulo-hyoid* ligament, and answers to the interopercular element of the osseous fishes' skull (Plate XXIX. [Plate 1], fig. 1, and Plate XXXI. [Plate 3], fig. 7, *m.h.l*).

The branchial apparatus is composed of two median pieces, the *first* and *second basibranchials* (Bb^1, Bb^2) ; of which the former is cartilaginous, pointed in front, where it is connected with the fibrous representative of the basihyal, broad behind, where it unites with the two ceratobranchials (Cb^1).

The second basibranchial is the only portion of the branchial apparatus which is ossified, and has been described above.

The stout *anterior ceratobranchials* (Cb^1) [1] meet in the middle line, between the first and second basibranchials. The broad, dorsal end of each articulates with the correspondingly broad, ventral end of the first *epibranchial* ($Ep.b^1$), which is curved, and tapers to a point at its dorsal extremity.

The *posterior ceratobranchial* (Cb^2) is a mere nodule of cartilage, which is connected, externally, with the anterior ceratobranchial and first epibranchial, and on its dorsal side articulates with the

[1] Fischer (*l.c.*, p. 19) considers that these represent the anterior and posterior ceratobranchials coalesced; but I see no evidence that such a process has taken place.

enlarged ventral end of the second epibranchial (*Ep.* b^2). The slender, slightly curved, third epibranchial (*Ep.* b^3) articulates with the enlarged ventral end of the second. There is no trace of a fourth epibranchial.

On comparing the cranium of *Menobranchus* with that of other *Amphibia*, one is at once struck (as Van der Hoeven has already remarked) by its many resemblances to that of *Proteus*.

In *Proteus*, the skull is similarly elongated and narrow, especially in the nasal and maxillary regions. The epiotic processes are prominent; and the suspensorium is inclined downwards and forwards at a like angle. The nasal, maxillary, and jugal bones are absent in *Proteus*, as in *Menobranchus*; the vomers and the palato-pterygoids have a similar disposition. In the general form and mode of attachment to the skull, in the rudimentary condition of the posterior ceratobranchial, in the presence of only three epibranchials, the hyoid and branchial apparatuses of *Proteus* closely accord with those of *Menobranchus*, though those of *Proteus* are, much more extensively ossified. In both genera the epiotic and opisthotic regions ossify and give rise to a distinct bone, the summit of which forms the epiotic process. Moreover, the chondrocranium of *Proteus* is, in all essential respects, similar to that of *Menobranchus*, though the trabeculæ are partially ossified where they lie between the nasal sacs.

In possessing prominent epiotic ossifications, which project as strong conical processes from the occipital region of the skull, *Menobranchus* and *Proteus* differ from all other existing Amphibia, and agree with the extinct Labyrinthodonts.[1] In the absence of the fourth epibranchial, *Proteus* and *Menobranchus* differ from *Siren*, *Siredon*, *Menopoma*, and *Amphiuma*. In the rudimentary condition of the second ceratobranchial they approach *Amphiuma* in which this element is absent.

In the structure of the chondrocranium, *Menobranchus* and *Proteus* differ from the Frog and from *Siredon* (the only Amphibia in which the chondrocranium has as yet been thoroughly examined) in the persistence, throughout life, of a far more embryonic type of structure. In fact, the skull of even the Lamprey is, in some respects, less embryonic than that of *Menobranchus*, the floor and roof of the occipital region having acquired a more complete chondrification in the Marsipobranch.

It is to the embryonic condition of the vertebrate skull

[1] *Siren* and *Amphiuma* have epiotic processes of a different form.

especially in the class to which *Menobranchus* belongs, that we must have recoùrse for an explanation of the structure of its primordial cranium.

If the cartilaginous skull of a tadpole, before it has lost its external gills, be compared with the persistent chondrocranium of *Menobranchus*, the general correspondence of the two becomes obvious (Plate XXXI. [Plate 3], fig. 3). There is a very large pituitary space bounded by the trabeculæ (*Tr*) at the sides. In front, the latter converge and coalesce into the internasal prolongations, which give rise to the mesethmoid of the adult Frog. But, in the tadpole, at this stage of its development, the "parachordal cartilages," which have been developed at the sides of the notochord, have united with one another and with the trabeculæ, and thus the pituitary space is much shorter than in *Menobranchus*. The cartilaginous skull of a tadpole of this age, in fact, has already obtained a higher development than it ever reaches in *Menobranchus*.

The auditory capsules are rounded behind, in the tadpole, and do not extend backwards as pointed processes beyond the level of the exoccipitals; in which respect the tadpole's skull is more frog-like, and less fish-like, than that of the adult *Menobranchus*.

In the tadpole's skull, the suspensorium is attached to the trabecula of its side, close to the point at which the latter passes into the parachordal cartilage. The cartilaginous band (*m*, Plate XXXI. [Plate 3], fig. 3), in fact, which passes into the trabecula, is the dorsal end of the mandibular arch, and corresponds with the pedicle of the suspensorium in *Menobranchus*, having the same relations to the ganglia and branches of the fifth and seventh nerves. In the adult Frog, the pedicle of the suspensorium has been carried outwards by the lateral growth of the auditory region of the skull, and is articulated by a joint[1] with the cartilage of this region, close to the outer extremity of the transverse arm of the parasphenoid. The inner process of the pterygoid lies on its ventral side, closely applied to it.

The elbow (*o*), by which the suspensorium of the tadpole abuts against the anterior and external face of the auditory capsule, evidently corresponds with the *otic process* of the suspensorium of *Menobranchus*. In the adult Frog, the suspensorium, which is ossified only at its mandibular end, forks, at its cranial end, into two branches or crura, the interspace between which is filled by fibrous tissue

[1] My friend Mr. Parker, F.R.S., in his remarkable memoir on 'The Structure and Development of the Skull of the Common Frog' (Philosophical Transactions, 1871), has given a different account of the origin of this singular articulation; but I believe I may say that he now agrees with me.

(Plate XXXI. [Plate 3], fig. 6). These crura, and the fibrous tissue which connects them, form the front wall of the tympanic cavity; the dorsal crus, which answers to the otic process, passes into the *tegmen tympani*, or roof of the tympanum, which is furnished by the outgrowth of the auditory capsule; the ventral crus is the pedicle of the suspensorium just mentioned.

Passing between the two crura (as Dugès long since pointed out) the seventh nerve enters the tympanum, closely applied to the inner wall of which (but not included in any Fallopian canal), it passes, above the level of the *fenestra ovalis*, over the *columella auris*. It takes, in fact, exactly the same course as in a mammal, except that it runs round the auditory capsule, instead of being included in a canal by the growth of the latter round it.

Some remarkable consequences appear to flow from the observed metamorphoses of the cranial end of the mandibular arch in the Frog. If the ossification which has already set in in the mandibular end of the suspensorium extended up into its dorsal crus, or otic process, we should have a quadrate bone, exactly like that of a Chelonian reptile. On the other hand, if the ventral crus became ossified continuously with the inner process of the pterygoid, and the basisphenoid were developed, we should have such a connexion of the pterygoid with the basisphenoid as exists in many Lizards and Birds.[1] Whence it appears to follow, that this part of the pterygoid represents the, morphologically, dorsal end of the mandibular arch, and that the dorsal end of the os quadratum is a secondary development of that arch, which becomes applied to the outer face of the auditory capsule.

The articular surfaces for Meckel's cartilage are corresponding points in both *Menobranchus* and the Frog's tadpole; but the *palato-pterygoid* process (*p*), which is rudimentary in the *Menobranchus*, and far apart from the antorbital process (*A.O*) (the intermediate space being occupied only by membrane, bone, and connective tissue), is, though equally short, completely fused with the antorbital process in the tadpole.

[1] Stannius ('Handbuch d. Zootomie,' 2te Auflage: "Die Amphibien," p. 36) remarks, in giving the general characters of the skull in the "Amphibia Dipnoa," that the more or less cartilaginous pterygoid arcade in these animals is always connected with the rest of the skull in three places: 1, with the suspensorium; 2, with the sphenoidal region of the skull; 3, with the lower part of the anterior and outer wall of the orbital cavity. Of these "the connexion with the sphenoidal region answers to the articulation of the pterygoid with the basisphenoid in most *Streptostylica* [Lacertilia and Ophidia], Birds, &c.; the connexion with the lower part of the anterior wall of the orbit corresponds with the union of the pterygoid with the maxilla and jugal by means of an *os transversum* in *Streptostylica* and Crocodiles."

There remain to be compared the orbital process (*Or*) of the suspensorium of the tadpole and the ascending process (*a*) of the suspensorium of *Menobranchus.*

It is clear that the orbital process, if it grew upwards and inwards towards the dorsal side of the trabecula, might very well cover in the orbito-nasal branch of the fifth nerve, as it actually does in *Menobranchus.* But then it would also cover in the third division of the fifth and the levator muscle of the mandible, internal and anterior to which it lies in *Menobranchus.*

For these reasons I do not identify the "orbital process" of the tadpole's suspensorium with the "ascending process" of that of *Menobranchus,*[1] though in some respects they are analogous.

In the tadpole, the tissue on each side of the notochord is so largely chondrified that it has formed a complete floor to the occipital and interauditory region of the skull, has roofed in the occipital region, and has coalesced with the auditory capsules; and the skull has attained this condition at a much earlier stage than that to which reference is here made.[2]

But I know of no condition of the skull of the Frog which is quite so instructive in its bearing on that of *Menobranchus* as is the skull of a *Triton* about the period at which it leaves the egg[3] (Plate XXXI. [Plate 3], figs. 2, 2*a*), or that of a larval Axolotl (Plate XXXI. [Platę 3], fig. 1).

Here the notochord occupies the centre of the future *basis cranii*, terminating in front in a rounded apex. The parachordal tissue exhibits no trace of chondrification; but it is very interesting to observe, on each side of it, the indication of an intermuscular septum, separating two myotomes, and thus indicating, so far, a segmentation of this region.

The auditory capsules are spherical sacs, which lie, quite isolated, on each side of the notochord, at some distance from it, and are not yet chondrified. The trabeculæ abut against the notochord posteriorly, but are wholly separate from any other structure. In front, they have begun to coalesce and to give rise to the broad internasal plate which is characteristic of the Salamandridea. On each side of them are seen the nasal sacs, with the minute posterior

[1] A corresponding process exists in *Proteus*, *Siredon*, *Menopoma* and *Amphiuma*.

[2] See my Croonian Lecture (Proc. Roy. Soc. 1858), and, for full details, Mr. Parker's Memoir in the 'Philosophical Transactions' for 1871, already referred to.

[3] The observations on which the following statements respecting *Triton* rest, were made in 1858; but I did not publish them, as I could not then obtain the materials for completing the history of the development of the Triton's skull. Perhaps I shall be more fortunate this spring.

nares opening into the cavity of the mouth. Behind, and external to, each trabecula is a stout cartilaginous rod, which obviously represents the suspensorium; but the dorsal end of this cartilage (*m*) though it lies close to the trabecula, has not yet coalesced with it, and the mandibular arch is therefore quite free. The external angle (*o*) corresponds in its relation to the auditory capsule with the part similarly marked in the Frog's tadpole, and in *Menobranchus*. At (*q*) is the articular surface for Meckel's cartilage (*Mck*); but neither "orbital," "ascending," nor "palato-pterygoid" processes are as yet developed.

The hyoidean arch (*Hy*, figs. 2, 2*a*) is as distinct and independent as are the mandibular and trabecular arches; it is an unjointed cartilage with a pointed dorsal end, which lies close to the auditory capsule. At its ventral extremity it coalesces with its fellow; while, behind, it is continuous with a median cartilage, which represents the basibranchials and ends in a long spatuliform style. From the sides of the median cartilage two ceratobranchials proceed, and are continued, the anterior into the first epibranchial, the posterior into the three other epibranchials. None of these parts are distinctly articulated, the future joints being, at most, faintly indicated. Sundry ossifications are visible in the fibrous tissue contiguous to the cartilages; thus the dentary (*D*) and splenial (*Spl*) pieces of the mandible, the squamosals (*Sq*), and the præmaxillæ (*Pmx*) (already one bone) have made their appearance.

The vomers (*Vo*), each of which bears two teeth, lie far apart, on the inner side of each nasal opening, and beneath the anterior end of the trabecula. Behind these are two dentigerous ossifications of the fibrous roof of the mouth, broad and rounded in front, but drawn out behind into a sort of tail, which is directed towards the suspensorium, though it does not reach the latter. These bones correspond with the anterior moieties of the palato-pterygoids of *Menobranchus*, and they occupy the same position as the palatines of the higher Vertebrata. But these bones, in fact, undergo very singular changes of position in the Salamanders. In the young *Siredon* (Plate XXXI. [Plate 3], fig. 1) they have the general form and relations which they exhibit in all known Salamandrine larvæ; and, so long as *Siredon* retains its branchiæ, no important change takes place; but in the abranchiate *Siredon* (*Amblystoma*) and in *Amblystoma carolinæ* dentigerous bones, obviously identical with these, occupy the position of the palatine bones of the Frogs, lying transversely to the axis of the skull immediately behind the posterior nares.[1]

[1] Profs. A. Duméril and O. C. Marsh have already noticed the change of position of these bones in Axolotls which became metamorphosed into *Amblystoma*.

In the common Tritons and Salamanders, on the other hand, these bones, as Dugès originally observed, gradually incline backwards and inwards, parallel with the base of the skull, coalesce with the vomers, and become the long dentigerous tail-like prolongations of the vomers, which adhere to the under surface of the parasphenoid. It can hardly be doubted that the so-called "sphenoidal" teeth of *Plethodon* and other Salamandridea are of the same nature.

Whatever direction the palato-dentary plates may take, however, they lose their primitive connexion with the pterygoid in all the Salamandridea, the anterior end of that bone and of its supporting cartilage moving outwards, and coming into connexion with the maxilla as it does in the Frogs.[1] The posterior nostril is, usually, bounded only by a cartilage, or ligament, representing the antorbital process.

As the development of the *Triton* advances, chondrification takes place in the base of the skull on each side of the notochord ; it extends backwards, to give rise to the occipital condyles, upwards, to form the occipital arch, and inwards, to constitute the basioccipital region ; and the auditory capsules coalesce with the posterior extremities of the trabeculæ and with the *parachordal* cartilage thus developed. Moreover the internasal or mesethmoidal cartilage gives off expansions above and below the nasal sacs, which become the roofs and floors of the nasal chambers. But a large membranous fontanelle persists between the trabeculæ in the basi- and presphenoidal regions ; and it is only in the Frogs that this intertrabecular or "pituitary" space appears to become completely chondrified.

Thus the chondrocranium of *Menobranchus* presents a little advance upon that of the larval *Triton* just leaving the egg, in so far as it possesses parachordal chondrifications, and in so far as the mandibular arch and the auditory capsules have coalesced with them and with the trabeculæ ; but it is inferior to the chondrocranium of *Siredon* and of the ordinary Salamanders in the absence of subnasal and supernasal alæ, and in the want of a complete cartilaginous occipital segment.

No known Elasmobranch, Ganoid, or Teleostean fish presents so incompletely developed a chondrocranium as that of *Menobranchus*. On the other hand, the latter is much like that of a Lamprey, if we leave the ossifications of the *Menobranchus* skull, and the accessory cartilages of the *Petromyzon*, out of consideration. And this fact, taken together with the curious resemblances in development between

[1] In the adult (branchiate) *Siredon* it is interesting to observe that the apex of the pterygoid cartilage already lies a little outside the outer margin of the palatine bone.

the Lampreys and the Amphibia (which are much closer than those between any of the higher Fishes and the Amphibia),[1] suggest to my mind the supposition that, in the series of modifications by which the Marsipobranch type has been converted into that of the higher fishes, the most important terms must have been forms intermediate in character between the *Dipnoi* and the *Marsipobranchs*. The skeleton of such a fish as *Ceratodus*, if it had a *Menobranchus*-like chondrocranium, would approach that of the Lampreys more than that of any fish known at present; and it is not difficult to imagine the steps by which such a fish might be built up upon the " lines " of a Lamprey.

The bearing of the structure of the chondrocranium in *Menobranchus*, the larval *Triton* and *Siredon* upon the theory of the skull is obvious.

It is plain that three morphologically distinct elements enter into the composition of the cranium in these animals :—

1. The *parachordal* elements or " investing masses " of Rathke, which stand in the same relation to the notochord, in the skull, as the formative tissue out of which the bodies of the vertebræ are developed, in the spinal column.

2. The *pleural* elements or visceral arches, which are divisible into trabecular, mandibular, hyoidean, and branchial.

3. The *paraneural* elements or capsules of some of the organs of the higher senses.

The brain-case is a complex structure, formed by the coalescence of elements belonging to all three classes; the face, by the metamorphosis of visceral arches only.

The occipital portion of the chondrocranium, which lies behind the auditory capsules, and which, by its ossification, gives rise to the proper exoccipitals in Amphibia, and, in addition, to the basioccipital and supraoccipital in Osseous Fishes and the higher Vertebrata, appears in all cases to result from the metamorphosis and ossification of parachordal elements.

On the other hand, that portion of the chondrocranium which lies in front of the auditory capsules is, in the Amphibia, formed by the coalescence and metamorphosis of the trabeculæ. It is by their vertical growth that the relatively high lateral walls of the cranium of the Frog are formed; it is by their coalescence in the ventral median line that the pituitary space becomes completely floored with cartilage in the same animal; and it is by the outgrowth of alary processes from the coalesced internasal, or mesethmoidal, portions of the trabeculæ, that the roof and floor of the Frog's nasal capsules are produced.

[1] Unfortunately we know nothing of the development of the *Dipnoi*.

Menobranchus is exceptional among the Amphibia in presenting no ossification of the substance of the trabeculæ in front of the pro-otic. In all the other genera, so far as I am aware, these structures are ossified to a greater or less extent in front of the exit of the optic nerves.

In *Proteus*, the ossification is internasal only; in *Siredon* and *Menopoma*, it is interorbital only; in *Siren*, there are two extensive interorbital ossifications, which send median prolongations into the internasal septum, and thus afford a transition to the fully developed sphenethmoid (or "os en ceinture" of Cuvier) of the Frogs.

I see no reason for doubting the homology of the paired interorbital ossifications of *Siredon* with the orbito-sphenoids of the higher Vertebrata; in which case, that portion of the basis of the skull which arises out of the coalescence of these parts of the trabeculæ, and is ossified into one mass with them, in the Frogs, must represent the presphenoid; and if this be so, the floor and side-walls of the skull, between the interorbital ossification and the pro-otic bones, must answer to the basisphenoid and the alisphenoid; while that which lies in front of the interorbital ossification must correspond with the median and lateral ethmoids of the higher Vertebrates.

In the Amphibia all these parts are formed by the gradual extension and subsequent metamorphosis of the trabeculæ. All the steps of gradual enlargement, apparent outgrowth, and metamorphoses of these primitively rod-like cartilages can be followed; and no part of the chondrocranium in these regions is formed independently of them.

This is all I intend to convey by the expression that the sphenoidal and ethmoidal regions of the skull are products of the growth and metamorphosis of the trabeculæ. If the questions be raised, Have the trabeculæ, when once formed, a quasi-independence? and do they grow into the adjacent tissues, as a tree pushes its roots into the soil? Or does not their extension and apparent growth arise rather from a chondrification of the pre-existing tissue in the immediate neighbourhood of the trabecular cartilage? it seems to me that no definite answer can be given to them.

In the larval *Triton* and *Siredon*, at the stage of development described above, for example, there is no complete cartilage either at the sides of the notochord, behind the trabeculæ, or in the ethmoidal region, in front of the trabeculæ. And it would seem that the cartilage which eventually exists in both these regions, arises in the same way—namely, by gradual chondrification of the tissue

beginning in that part which is in contact with the trabecula, and extending backwards, or forwards, as the case may be. And it may be said that if the apparent growth of the trabecula into the parachordal region is not to be described as a backward growth of the trabecula, so neither is the alisphenoidal, or orbito-sphenoidal, cartilage in the side-wall of the skull to be described as an upward growth of the trabecula ; and this view would receive support from any cases in which the orbito-sphenoids, or alisphenoids, take their origin by independent development in the side-walls of the skull.

The same difficulty arises when we attempt to determine the nature of the cartilaginous walls of the nasal chambers. To all appearance these, in all Amphibia which possess them, grow out of the coalesced trabeculæ. But if it be said that they are independent chondrifications of the capsule of the olfactory sac, like those which certainly take place in the case of the eye and of the ear, and that the appearance of outgrowth from the trabeculæ is simply due to the fact that this independent process of chondrification begins in contiguity with the trabecula and extends outwards, I do not know that there is any means of deciding the question at present.

No doubt the perfect independence of the sclerotic and of the wall of the primitive auditory sac, lends countenance to the hypothesis that the olfactory sacs are provided with similar proper walls. And it is easy to imagine that the antorbital process and the ethmoidal alæ, taken together, may represent the sclerotic and the periotic cartilages ; but it is very difficult to find proof of the fact, and, until such proof is produced, it may be better to enumerate the auditory capsules, alone, among the *paraneural* elements of the skull.

2. *The Heart.*

The heart of *Menobranchus* has been described by Mayer and by Van der Hoeven in the works already cited.

According to the former writer (*l.c.*, p. 83),

" The heart is shaped like that of *Proteus anguinus*, and lies free in the pericardium. It consists of a ventricle and an auricle with two appendices (Herzohren), one on each side. The *truncus arteriosus* arises, as in the Batrachians, from the right corner of the ventricle. Upon each side, a *saccus venosus* appears beneath the appendix of the auricle of its side, and receives the corresponding superior vena cava. But in the pericardial chamber there are two inferior cavæ, formed by the division of the main trunk, which enters the pericardium at the upper edge of the liver. The right *saccus venosus* finally opens into

the left; and out of this an aperture leads into the simple auricle, which, however, as has been said, presents two appendices.

"Near the sinu-auricular aperture the auriculo-ventricular opening (*ostium venosum*) leads into the ventricle. There are two auriculo-ventricular valves, with an interposed cleft. The ventricle is simple, but partially divided above by a median projection of its fleshy wall. The *bulbus aortæ* gives off two branches on each side; these pass towards the branchial arches; and the posterior again divides. The three branchial arteries thus produced run along the anterior edges of the branchial arches to the branchial plumes; from these the branchial veins pass along the posterior edges of the branchial arches, and, after uniting into a single trunk on each side, give rise to the *aorta descendens.* The existence of an anastomosis between the trunks of the artery and that of the vein of each branchia was indistinct; but small branches went to the branchial filaments.

"The pulmonary arteries arise from the trunk into which the branchial veins unite on each side. The pulmonary veins open, on each side, into the corresponding inferior vena cava. In addition, I found, but only on the left side, that a vein arose from the posterior vesicular end of the lung, which, uniting with a superior ovarian vein, passed directly into the *vena cava inferior*, as Rusconi has represented to be the case in *Proteus anguinus.* On the right side, a vein from the stomach opens into the pulmonary vein."

Van der Hoeven adds to this description a more precise account of the *truncus arteriosus* (which he terms arterial trunk, "slagaderlijken stam"), and its terminal dilatation into an elongated oval *bulbus arteriosus*, (*l. c.* p. 30):—"At the origin of the *truncus arteriosus* lie three semilunar valves, and higher up beneath the *bulbus* three more. In the *bulbus* itself is a freely projecting solid plate, by which its cavity is almost divided into two semicanals."

He further states that the auricle "is divided by an imperfect septum;" but he gives no account of the form or structure of this septum.

In the specimen dissected by me, the heart (Plate XXXII. [Plate 4] figs. 1 to 6) was lodged in an oval pericardial cavity, situated between the styliform second basibranchial and the curious chondrification of the *linea alba* and of the adjacent parts of the intermuscular septa, which Mayer (*l. c.*, p. 85) justly interpreted as the sternum. Thick masses of longitudinal muscular fibres lie or each side of the pericardium, and represent the sterno-hyoi muscles.

The heart consists of a dorsal division, composed of the *sin*

venosus (*S*) and of the auricles (*A*), and of a ventral division, consisting of the ventricle (*V*) and the *truncus arteriosus* (*T. a*). The *sinus venosus* lies immediately over the posterior half of the ventricle, and is formed by the junction of the two inferior caval trunks described by Mayer.

The right and left superior cavæ (*R.s.v.c*, *L.s.v.c.*) open into these at their passage into the *sinus venosus*, and might fairly be said to communicate directly with the latter. The sinu-auricular aperture is situated in the right half of the posterior wall of the spacious auricular cavity. Though its lips project somewhat into the auricular cavity, they can hardly be regarded as truly valvular.

The auricular chamber is very spacious, and extends forwards nearly as far as the anterior end of the pericardium. It lies above the *truncus arteriosus* in front, and the anterior half of the ventricle behind. On each side, it is produced into a saccular dilatation, which extends over the *truncus* and ventricle to the ventral wall of the pericardium on the left side, but is much less developed on the right side, where it leaves the ventricle uncovered. The wall of the right dilatation presents three or four longitudinal folds.

On the dorsal face of the *sinus venosus*, between the two superior cavæ and the diverging inferior caval trunks, lies the pulmonary vein (*P. v.* fig. 4). It is very narrow posteriorly, but dilates in front, and, turning to the left, opens into the posterior part of the auricular cavity, to the left of the middle line.

The existence of the anomalous arrangement of the pulmonary veins in the specimen described by Mayer is therefore rendered doubtful, though I am unwilling to suggest that so accurate an observer was altogether mistaken.

The right wall of the dilatation of the pulmonary vein is continued downwards, forwards, and to the left side, nearly as far as the dorsal lip of the auriculo-ventricular aperture, as a delicate plate formed of muscular fibres, coated, on each side, by a layer of the cardiac epithelium. This plate represents the auricular septum; but it extends for but a very short distance forwards, and then, as it were, frays out into separate branched muscular bands, each of which is invested by its own epithelial cells. On the dorsal side, these bands proceed to be attached to the wall of the auricle about midway between its anterior and its posterior ends; but the ventralmost band makes an arch across the auriculo-ventricular aperture, and passes into a single muscular pillar, which is attached on the ventral side of that aperture. Anteriorly, this column branches out, and its divisions attach themselves to the left wall of the auricle and unite with the

ramifications of the muscular bands proceeding from the dorsal side of the auriculo-ventricular opening (figs. 4 & 5).

The "plate," the "pillar," and the branched muscular bands which proceed from them, which have just been described, are all that represent the septum of the auricles, which therefore can have but little efficacy as a partition between the pulmonary and the systemic venous blood. These two kinds of blood must mix freely through the wide meshes of the network of fibres invested by epithelium; and it is only above and behind, where the meshes become closer and the network gradually passes into the impervious "plate," that the pulmonary blood can be guided to the auriculo-ventricular aperture by a special channel.[1]

The auriculo-ventricular valves are mere narrow folds of the endocardium, bounding the margins of the auriculo-ventricular aperture, which is triradiate, in consequence of a notch in its ventral lip.

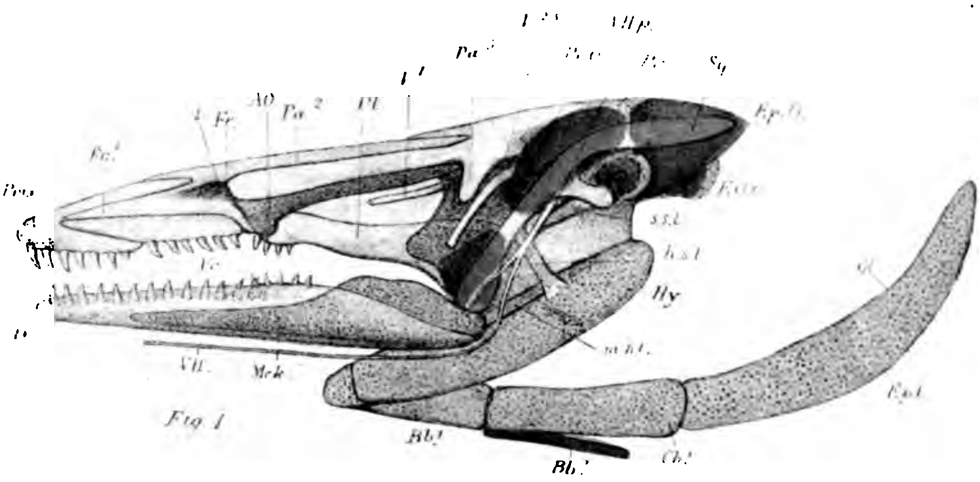
The ventricle is oval in form; its cavity is small, directed transversely, and bounded by thick, spongy, muscular walls. The left end of the cavity communicates with the auricle; the right end opens into the elongated *truncus arteriosus.* The moiety of this *truncus* which lies nearest the heart is a tube, divided by a slight transverse constriction into two but little-marked dilatations.

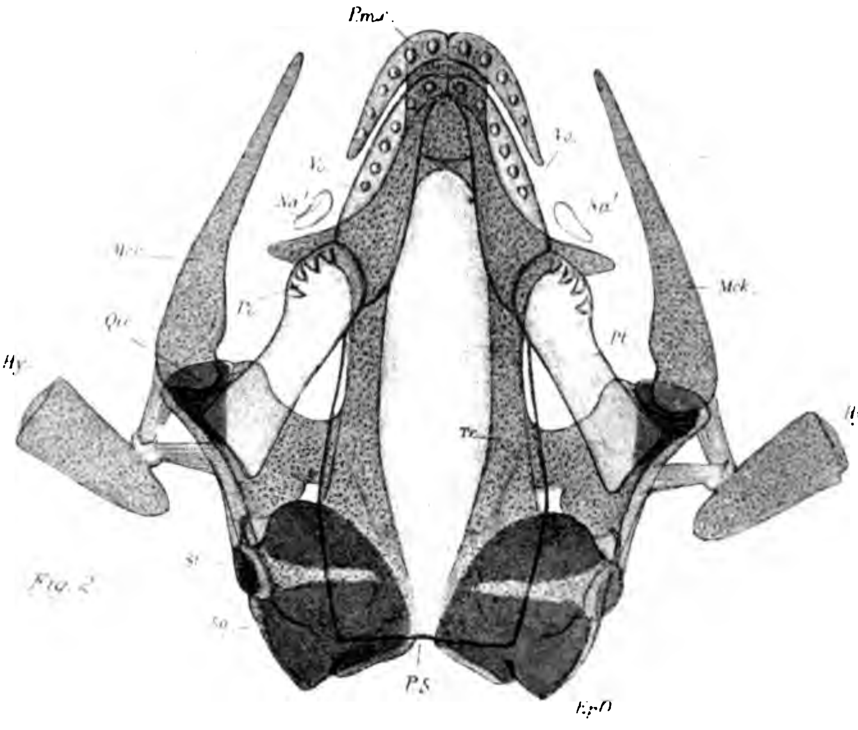
As Van der Hoeven has stated, there are three semilunar valves set in a transverse row in the first dilatation, just above the aperture of communication with the ventricle, while three other such valves are disposed across the middle of the second dilatation. The division of the *truncus arteriosus* which contains these valves may be termed the "*pylangium.*"[2] The bulb-like termination of the *truncus arteriosus*, on the other hand, is divided into four canals by two septa disposed at right angles to one another, and is clearly formed by the coalescence of the aortic arches. It may therefore be termed the "*synangium.*"

[1] Stannius ('Handbuch,' p. 216, note) states that, according to his own and Hyrtl's observations, the separation of the auricles is apparently incomplete (*anscheinend* unvollkom men) in *Proteus*, *Menobranchus*, and *Siren.* As regards *Proteus*, in the only specimen have dissected I have failed to find any trace of a septum; but in *Siren* I have found complete, and extending between the auriculo-ventricular valves to terminate with a fr edge, just as in the Frogs. According to Fritsch (' Zur vergleichende Anatomie der Amp bienherzen," Archiv für Anatomie, 1869), the septum is sometimes very imperfectly develo in adult (mässig kräftige) specimens of *Rana temporaria* and *R. esculenta.* A series of F examined in the spring of 1860 exhibited this condition. But in these cases the septur reduced to a fold of the auricular wall, while in the specimen of *Menobranchus* he scribed the septum extends nearly to the auriculo-ventricular aperture, but is perforat have not met with the condition of the septum described by Fritsch in adult Frogs.

[2] πύλη, a gate, and ἀγγεῖον a vessel.

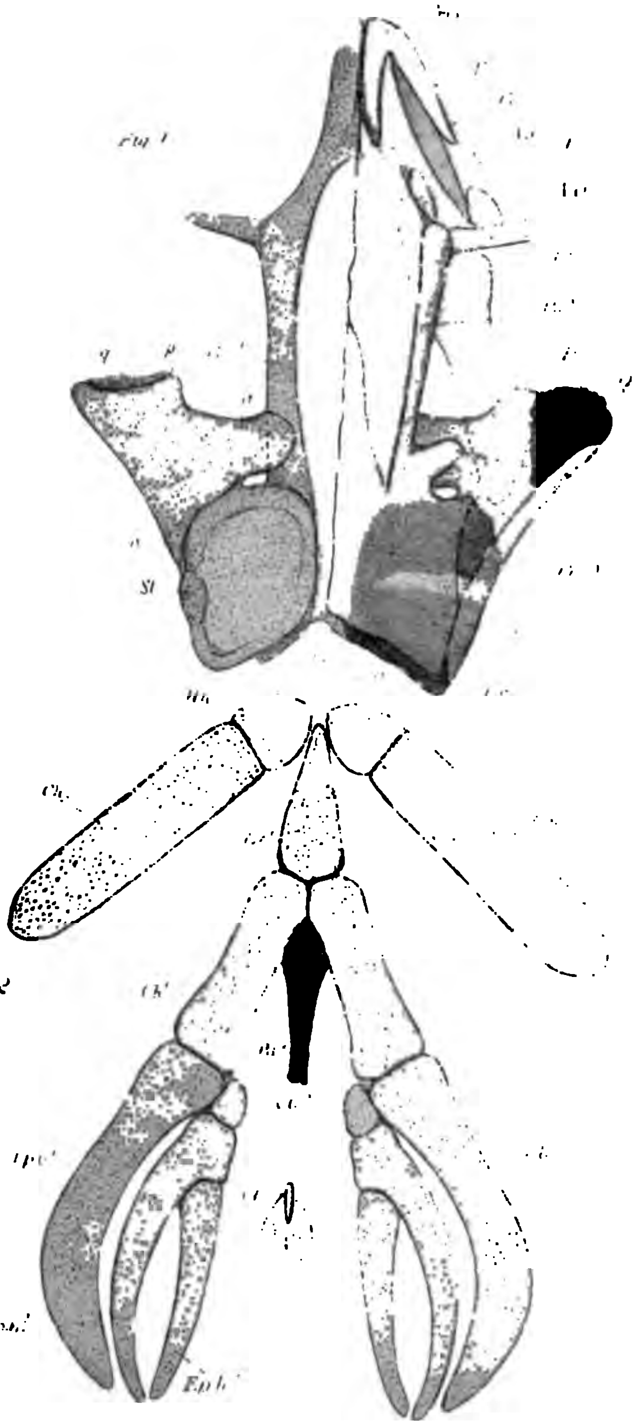
[PLATE 1.]





MENOBRANCHUS

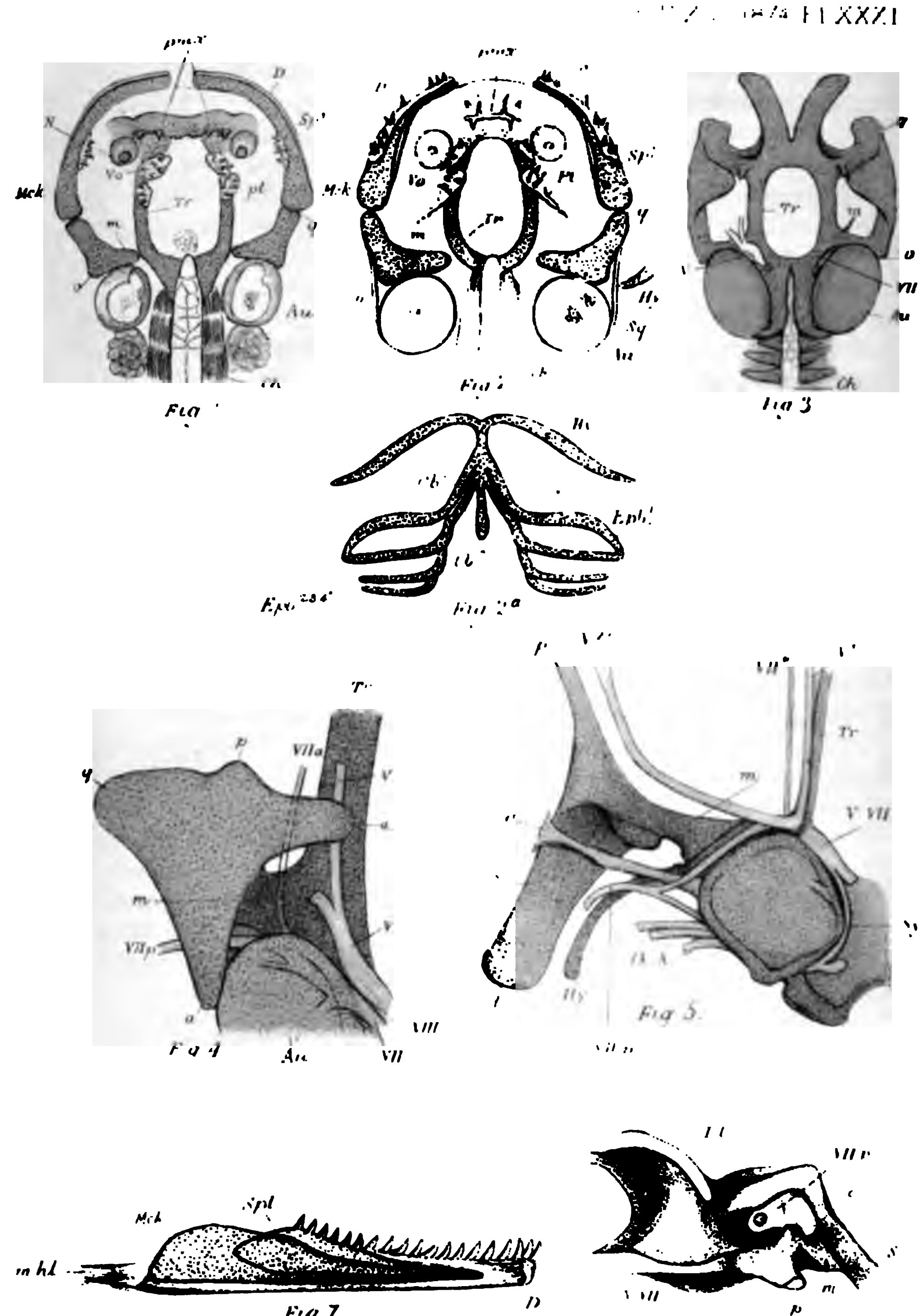
[PLATE 2.]



W H Wesley Lith

MENOBRANCHUS

[PLATE 3.]



W H Wesley lith

M & N Hanhart imp

MENOBRANCHUS. RANA. SIREDON. TRITON

Throughout the Amphibia these two constituents of the *truncus arteriosus* are readily distinguishable, though they vary very much in form and proportions, the pylangium being longest in proportion to the synangium in the Anura, shortest in the *Peromela*. Moreover, in the higher *Urodela* and the *Anura*, the pylangium becomes complicated by the development of a longitudinal septum, which extends from the anterior to the posterior set of valves, and imperfectly divides the cavity into two chambers.

DESCRIPTION OF THE PLATES.

PLATE XXIX. [PLATE 1].

Fig. 1. Side view of the skull of *Menobranchus lateralis*.
2. Ventral view of the same.

PLATE XXX. [PLATE 2].

Fig. 1. Dorsal view of the same, all bony matter being removed from the left half of the skull.
2. Ventral view of the hyoidean and branchial apparatus.

All the figures of the skull are magnified three times. In all, cartilage is coloured blue, and cartilage-bone light brown. Membrane-bone is left uncoloured.

The signification of the letters is the same throughout.

Cartilage-bones.—*E. O*, exoccipital; *Ep. O*, epiotic and opisthotic; *Pr. O*, prootic; *Qu*, quadrate; *St*, stapes; *Bb²*, second basibranchial.

Membrane-bones.—*Pa*, parietal, with its three processes *Pa¹*, *Pa²*, *Pa³*; *Sq*, squamosal; *Fr.* frontal, with its antero-lateral prolongation, *Fr.* 1; *Pmx*, præmaxilla; *Vo*, vomer; *Pa*, *Pt*, coalesced palatine and pterygoid; *P.S*, parasphenoid; D, dentary; *Sp*, splenial.

Chondrocranium.—*Tr*, trabecula; *A.o*, antorbital process; *q*, quadrate process; *p*, pterygoid process; *a*, ascending process; *o*, otic process; *m*, pedicle of the suspensorium; *Mck*, Meckel's cartilage; *Hy*, hyoid arch; *Hh*, hypohyal; *Ch*, ceratohyal; *Bb¹*, first basibranchial; *Cb¹*, first ceratobranchial; *Epb¹*, first epibranchial; *Cb²*, second ceratobranchial; *Epb²*, *Epb³*, second and third epibranchials.

Ligaments.—*m.h.l*, mandibulo-hyoid; *h.s.l*, hyo-suspensorial; *s.s.l*, suspensorio-stapedial.

Nerves and foramina for nerves; I, olfactory foramen; V, orbito-nasal branch of the trigeminal; $V^{2,3}$, second and third division of the trigeminal; VII.*p*, posterior division of the portio dura.

PLATE XXXI. [PLATE 3].

Fig. 1. Chondrocranium of a larva of *Siredon*. Fig. 2, of *Triton*, ventral aspect; fig. 2*a*, hyoidean and branchial apparatus of the same *Triton*-larva.

In these larvæ the walls of the auditory capsules were not yet chondrified. Letters as before, except *N*, nasal sac; *Ch*, notochord.

3. Chondrocranium of a tadpole, dorsal aspect. V, trigeminal ganglion; VII, ganglion of the seventh nerve.

Fig. 4. The suspensorium of *Menobranchus*; and fig. 5, that of *Rana esculenta*, with the adjacent parts decalcified. In *Rana* the dorsal crus, or otic process, has been removed to show the course of the posterior division of the seventh nerve (VII.*p*) over the columella auris, *C.a.* VII.*a*, the anterior division, palatine or Vidian nerve; *Sy*, commissural cord (sympathetic ?) connecting the ganglion of the glosso-pharyngeal and pneumogastric (VIII. IX) with the coalesced ganglia of the fifth and seventh nerves (V, VII).

6. A transverse section of the left half of the decalcified skull of *Rana esculenta*, to show:—*m*, the inferior crus or pedicle of the suspensorium; *o*, its superior crus continuous with the tegmen tympani, *T.t*, and the posterior division of the seventh nerve, VII.*p*, passing between these; V, VII indicate the place occupied by the conjoined ganglia of the fifth and seventh nerves.

7. The left ramus of the mandible of *Menobranchus*, viewed from within.

PLATE XXXII [PLATE 4].

Fig. 1. ventral, fig. 2 left lateral, fig. 3 right lateral view of the heart of *Menobranchus lateralis*. Fig. 4. Dorsal aspect of the heart, with the auricles, sinus venosus, and cavæ laid open. Magnified four times.

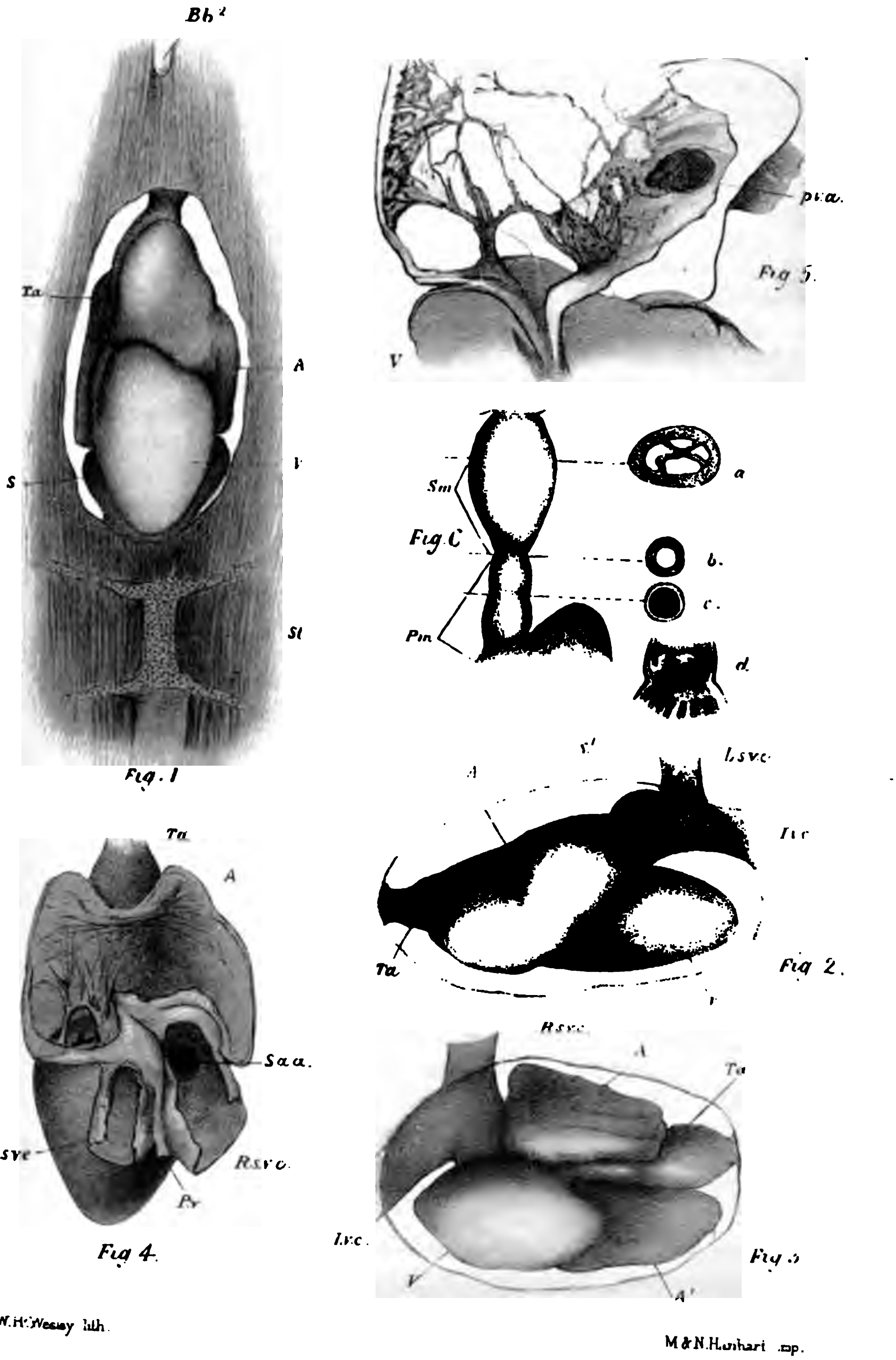
5. Enlarged view of the septum of the auricles, from the left side.

6. The truncus arteriosus, with transverse sections (*a*, *b*, *c*), and laid open to show the posterior pylangial valves (*d*).

S, sinus venosus; *A*, auricular segment; *V*, ventricle; *T.a*, truncus arteriosus; *L.s.v.c*, *R.s.v.c*, left and right superior venæ cavæ; *I.v.c*, inferior vena cava; *S.a*, sinu-auricular aperture; *P.v*, pulmonary vein; *p.v.a*, opening of the pulmonary vein into the left auricle; *Pm*, pylangium; *Sn*, synangium.

[PLATE 4.]

P. Z. S. 1874. Pl. XXXII.



W. H. Wesley lith.

M & N. Hanhart imp.

MENOBRANCHUS.

II

NOTE ON THE DEVELOPMENT OF THE COLUMELLA AURIS IN THE AMPHIBIA

Nature, vol. xi., 1875, *pp.* 68, 69. (*Read at the Meeting of the British Association at Belfast, August 25th,* 1874.)

IN his paper "On the Structure and Development of the Skull of the Common Frog" (Phil. Trans. 1871), Mr. Parker states that, in the fourth stage of the tadpole,[1] "the hyoid arch has made its second great morphological change; it has coalesced with the mandibular pier in front and with the auditory capsule above (Plate V., Figs. 1—4, and Plate VI., Fig. 8, *s.h.m.*, *i.h.m.*). The upper part, or supra-hyomandibular (*s.h.m.*), is attached to the auditory sac much lower down and more outward than the top of the arch in front. . . . This upper distinct part is small; it answers to only the upper part of the Teleostean hyomandibular; there is a broad sub-bifid upper head answering to the two ichthyic condyles, then a narrow neck, and then behind and below an 'opercular process' (*op.p.*) Below this the two arches are fused together; but the hyoid part is demonstrated just above the commencement of the lower third, by the lunate fossa for the 'styloid condyle' (Plate V., Figs. 2 and 4, *st. h.*)" (pp. 154, 155).

In the sixth stage:—"The supra-hyomandibular (Fig. 3, *s.hm.*) has become a free plate of cartilage of a trifoliate form" (p. 164).

In the seventh stage:—"The 'supra-hyomandibular, losing all relation to the hyoid arch, becomes now part of the middle ear. . . . The *essential* element of the middle ear, the stapes (*st*), was seen in the fourth stage; the condyles and opercular process of the hyomandibular are now being prepared to form an osseo-cartilaginous chain from the 'membrana tympani' to the stapes. Under these conditions

[1] That is, when there is a branchial aperture only on the left side, and the hind limbs are rudimentary or very small.

a new nomenclature will be required ; and this will be made to depend upon the *stapedial* relationship of the chain, notwithstanding its different morphological origin.

"I shall now call the lobes of this trifoliate plate of cartilage as follows—namely, the antero-superior 'supra-stapedial,' the postero-superior 'medio-stapedial,' and the freed opercular process 'extra-stapedial' (*s.st.*, *m.st.*, *e.st.*)

"The stapes (*st.*) sends no *stalk* forwards to meet the new elements, but they grow towards it ; this will be seen in the next stage" (pp. 169, 170).

As the question of the origin of the *columella auris* in the *Vertebrata* is one of considerable morphological importance, I have devoted a good deal of time, during the past summer, to the investigation of the development of this structure in the frog, and it is perhaps some evidence of the difficulty of the inquiry, that my conclusions do not accord with those enunciated by Mr. Parker, in the very excellent and laborious memoir which I have cited

I find, in the first place, that there is no coalescence of the mandibular with the hyoidean arch, the latter merely becoming articulated with the former.

Secondly, Mr. Parker's "supra-hyomandibular" is simply an outgrowth of the mandibular arch from that elbow or angle which it makes, when the pedicle by which it is attached to the trabecula passes into the downwardly and forwardly inclined suspensorial portion of the arch. This outgrowth attaches itself to the periotic capsule, and, coalescing with it, becomes the *otic process*, or "superior crus of the suspensorium" of the adult frog.

The hyoid arch, seen in the fourth stage, elongates, and its proximal end attaches itself to the periotic capsule, in front of the fenestra ovalis and close to the pedicle of the suspensorium, which position it retains throughout life.

The *columella auris* arises as an outgrowth of a cartilaginous nodule, which appears at the anterior and superior part of the fenestra ovalis, in front of and above the stapes, but in immediate contact with it. It is to be found in frogs and toads which have just lost their tails, in which the gape does not extend further back than the posterior margin of the eye, and which have no tympanic cavity, as a short and slender rod which projects but very slightly beyond the level of the stapes, its free end being continued into fibrous tissue, which runs towards the suspensorium, beneath the portio dura, and represents the suspensorio-stapedial ligament of the *Urodela*.

This rod elongates, and its anterior or free end is carried outwards,

in proportion as the tympano-eustachian passage is developed. At the same time, the free end becomes elongated at right angles to the direction of the rod, and gives rise to the "extra-stapedial" portion, which is imbedded in the membrana tympani. Ossification takes place around the periphery of the middle of the rod ; thus the medio-stapedial is produced. The inner portion becomes the rounded, or pestle-shaped, supra-stapedial, but retains its primitive place and connections, whence we find it in the adult articulated in a fossa in that part of the periotic capsule which forms the front boundary of the fenestra ovalis, but in close contact with the stapes.

The *columella auris* of the frog, therefore, is certainly not formed by the metamorphosis of any part of either the mandibular or the hyoidean arches, such as they exist in the fourth stage of larval development.

It may be said further, that the *columella* undoubtedly *seems* to be developed from the side walls of the auditory capsule in the same way as the stapes, and some appearances have led me to suspect that it is originally in continuity with the stapes, but I am not quite sure that such is the case. Are we to conclude, therefore, that the columella is a product of the periotic capsule, such as the stapes has been assumed to be?

Here, I think, there is considerable ground for hesitation. It appears to me that the stapes is not so much "cut out" of the cartilaginous periotic capsule as the result of the chondrification of a portion of that capsule which remains unchondrified longer than the rest. Moreover, the *Urodela* all possess a band of ligamentous fibres which extends from the stapes to that part of the suspensorium with which the hyoid is connected, and to the hyoid itself. It is conceivable, and certainly not improbable, that this stapedio-suspensorial ligament represents the dorsal extremity of the hyoidean arch. But the *columella auris*, in its early condition in the frog, so nearly resembles the stapedio-suspensorial ligament partially chondrified, that it is hard to suppose that one is not the homologue of the other ; in which case the columella, and even the stapes itself, may, after all, represent the metamorphosed dorsal end or the hyoidean arch of the hyomandibular of a fish. And it must be admitted that the relations of the portio dura nerve to the hyomandibular in such a fish as the Ray speak strongly in favour of this view.

III

PRELIMINARY NOTE UPON THE BRAIN AND SKULL OF *AMPHIOXUS LANCEOLATUS*.

Proceedings of the Royal Society of London, vol. xxiii., 1875, *pp.* 127–132.
(*Received December* 17*th*, 1874.)

THE singular little fish *Amphioxus lanceolatus* has been universally regarded as an extremely anomalous member of the Vertebrate series by reason of the supposed absence of renal organs and of any proper skull and brain. On these grounds, chiefly, Agassiz proposed to separate it from all other fishes, and Haeckel, going further, made a distinct division of the Vertebrata (*Acrania*) for its reception; while Semper,[1] in a lately published paper, separates it from the Vertebrata altogether.

In a recent communication to the Linnean Society, I have described what I believe to be the representative of the ducts of the Wolffian bodies, or "primordial kidneys" of the higher Vertebrata, in *Amphioxus*; and I propose, in this preliminary notice, to point out that although *Amphioxus* has no completely differentiated brain or skull, yet it possesses very well marked and relatively large divisions of the cerebro-spinal nervous axis and of the spinal column, which answer to the encephalon and the cranium of the higher Vertebrata.

The oral aperture of *Amphioxus* is large, of a long oval shape, and fringed by tentacles, external to which lies a lip, which is continuous behind with the ventro-lateral ridge of the body. The oral chamber is spacious, and extends back to the level of the junction between the sixth and seventh myotomes (fig. A). Here it is divided from the branchial cavity by a peculiarly constructed muscular *velum palati*, the upper attachment of which to the ventral aspect of the sheath

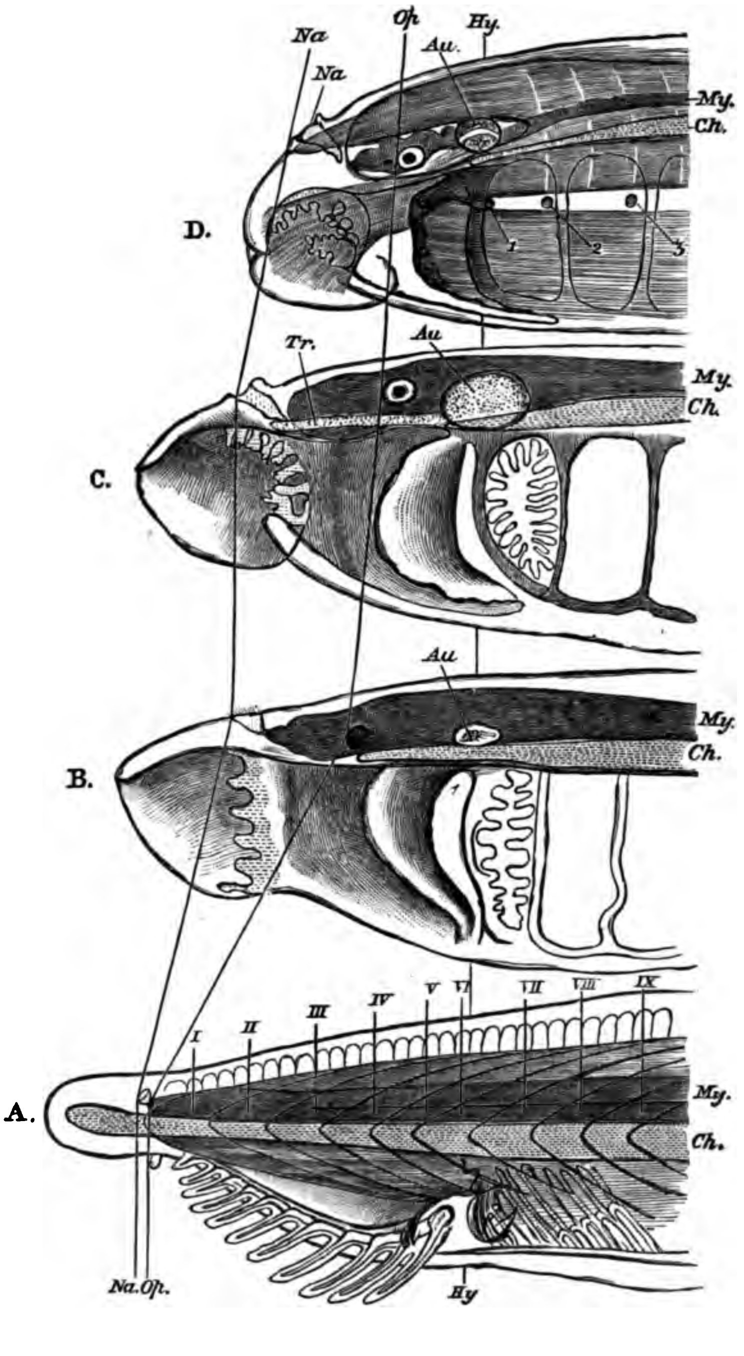
[1] "Die Stammverwandtschaft der Wirbelthiere und Wirbellosen," Arbeiten aus dem zool.-zootom. Institut in Würzburg, Bd. ii. 1874, p. 42.

of the notochord lies vertically below the anterior angle of the seventh myotome.

Eight pairs of nerves are given off from the cerebro-spinal axis as far as this point. The eighth, or most posterior of these, which, for convenience, may be called *h*, passes out between the sixth and seventh myotomes, and runs down parallel with the lateral attachment of the velum. The next five (*g*, *f*, *e*, *d*, *c*) pass out between the first six myotomes, and are distributed by their dorsal and ventral branches to those myotomes, to the integument and to the walls of the buccal cavity. The foremost two nerves (*b* and *a*) pass in front of the first myotome, and the nerve *a* runs parallel with the upper side of the notochord to the end of the snout, giving off branches to that region of the body which lies in front of the mouth. This nerve lies above the eye-spot.

In the Marsipobranch fishes *Myxine* and *Ammocœtes* (now known to be a young condition of *Petromyzon*) a velum also separates the buccal from the branchial cavity (figs. B, C, D). But this velum is in connexion with the hyoidean arch. The resemblance of the buccal cavity, with its tentacles, in *Ammocœtes* to the corresponding cavity in *Amphioxus* is so close that there can be no doubt that the two are homologous. In the *Ammocœtes* there is a hyoidean cleft which has hitherto been overlooked. The auditory sac lies at the dorsal end of the arch and above the dorsal attachment of the velum. The latter, therefore, corresponds with the auditory region of the skull, and the nerve *h* should answer to the last of the præauditory cranial nerves, which is the *portio dura*. Assuming this to be the case, though the detailed homologies of the cranial nerves of the higher Vertebrata are yet to be worked out, it follows that the segment of the cerebro-spinal axis which in *Amphioxus* lies between the origin of the nerve *h* and the eye, answers to all that part of the brain which lies between the origin of the seventh nerve of *Petromyzon* and the optic nerve. Consequently, the lateral walls of the neural canal in the same region answer to that region of the skull in *Petromyzon* which lies between the origin of the seventh and the origin of the optic nerve. Hence, as each myotome of *Amphioxus* represents the corresponding portion of a protovertebra, it follows that the same region of the skull in the Lamprey and other Vertebrata represents, at fewest, six protovertebræ, almost all traces of which are lost, even in the embryo condition of the higher Vertebrata.

It may further be concluded that the several pairs of nerves which leave the cerebro-spinal axis, between those which answer to the *portio dura* and the optic nerve, in *Amphioxus*, are represented by the third,



Na
Oph
Hy.
Au.
Na
My.
Ch.
D.
1
2
3
Tr.
Au
My.
Ch.
C.
Au
My.
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I
II
III
IV
V
VI
VII
VIII
IX
A.
My.
Ch.
Na.Op.
Hy

fourth, fifth, and sixth pairs of cranial nerves of the higher Vertebrata. The nerve *a*, in fact, has the characteristic course and distribution of the orbito-nasal division of the trigeminal; while, without at present drawing a closer parallel, it is easy to see that the nerves *b*, *c*, *d*, *e*, *f*, and *g*, with their respective myotomes, supply the requisite materials for metamorphosis into the oculomotor, pathetic, trigeminal, and abducens nerves, with the muscles of the eye and of the jaws, in the more differentiated vertebrate types.

Thus, that part of the cerebro-spinal axis of *Amphioxus* which lies in front of the seventh myotome answers to the præauditory part of the brain in the higher Vertebrata, and the corresponding part of the head to the trabecular region of the skull in them. On the other hand, from the seventh myotome backwards, a certain number of segments answer to the post auditory, or parachordal region of the skull of the higher Vertebrata.

The answer to the question, how many? involves sundry considerations. It must be recollected that though the branchial chamber of *Amphioxus* is the homologue of the branchial chamber of other Vertebrata, it does not necessarily follow that the imperfect branchial skeleton of *Amphioxus* corresponds with their branchial skeleton. The branchial skeleton of the higher Vertebrata consists of cartilaginous rods, which seem to be developed in the somatopleure, and to be homologous with the ribs, while the branchial skeleton of *Amphioxus* consists of fibrous bands apparently developed in the splanchnopleure.

The branchial arches of the higher Vertebrata, in accordance with their essentially costal nature, receive their innervation from the glossopharyngeal and pneumogastric nerves, which are homologues of spinal nerves; and, in seeking for the posterior limits of that region in *Amphioxus* which corresponds with the skull and brain in other Vertebrates, we must only take into account as many pairs of those nerves which arise from the cerebro-spinal axis as we know are, in the Vertebrata next above *Amphioxus*, devoted to the branchial arches. In none of these are there more than seven pairs of branchial arches; so that not more than eight myotomes (and consequently protovertebræ) of *Amphioxus*, in addition to those already mentioned, can be reckoned as the equivalents of the parachordal region of the skull in the higher Vertebrates. Thus it would appear that the cranium of the latter is represented by those segments of the body of *Amphioxus* which lie in front of the fifteenth, counting from before backwards, and that their cranial nerves are represented by the corresponding anterior pairs of nerves in *Amphioxus*.

In all Vertebrata above *Amphioxus* the nerves which answer to the seven posterior pairs in *Amphioxus* unite into one or two trunks on each side, and give rise to the nerves called pneumogastric and glosso-pharyngeal; and, as these pass out of the skull in front of the occipital segment, it would appear that this segment is, in the main, the result of the chondrification, with or without subsequent ossification, of the fourteenth protovertebra.

There is no evidence, at present, that the ear-capsule represents a modification of any part of the vertebral skeleton, nor that the trabeculæ are anything but an anterior pair of visceral arches. And if these parts have nothing to do with centra, or arches, of vertebræ, it follows that the numerous protovertebræ, which lie in front of the fourteenth in *Amphioxus*, are represented only by muscles and nerves in the higher Vertebrata.

The anterior end of the cerebro-spinal axis of *Amphioxus* answers to the *lamina terminalis* of the thalamencephalon of the higher Vertebrata, the cerebral hemispheres and olfactory lobes remaining undeveloped.

If the auditory nerve is, as Gegenbaur has suggested, the dorsal branch of a single nerve which represents both the *portio dura* and the *portio mollis*, the auditory organ of *Amphioxus* is to be sought in connexion with the dorsal branch of its eighth nerve. I have found nothing representing an auditory organ in this position; and I can only conclude that *Amphioxus* really has no auditory apparatus. In all other respects, however, it conforms to the Vertebrate type; and considering its resemblance to the early stages of *Petromyzon* described by Schulze, I can see no reason for removing it from the class Pisces. But its permanently segmented skull and its many other peculiarities suggest that it should be regarded as the type of a primary division or subclass of the class Pisces, to which the name of *Entomocrania* may be applied, in contrast to the rest, in which the primary segmentation of the skull is lost, and which may be termed *Holocrania*. On a future occasion I propose to show in what manner the skull of the Marsipobranch is related to that of the higher Vertebrata, and more especially to the skull of the Frog in its young tadpole state.

EXPLANATION OF THE FIGURES.

A, C, D are diagrammatic, but accurate, representations of the anterior part of the body in *Amphioxus* (A), in an *Ammocœte* 1·6 inch long (C), and in a fully grown *Ammocœte* 5·7 inches long (D). B is a copy of the furthest advanced stage of the young *Petromyzon planeri* six weeks after hatching, as figured by Schultze in his memoir on the development of that fish. The figures are magnified to the same vertical dimension, so as to afford a means of estimating, roughly, the changes in the proportional growth of the

various parts of the head of the Lamprey in its progress from the embryonic towards the adult condition. In C, the brain is already differentiated into the three primary vesicles and the vesicles of the cerebral hemispheres, though they are not shown, the whole brain being merely indicated by the dark shading. The trabeculæ (*Tr*), which have already united in front, are indicated, but not the semilunar ethmoidal cartilage, which lies above and behind the nasal sac. In D, neither the ethmoidal nor the trabecular cartilages are shown, but the contour of the brain is indicated; and the manner in which the longitudinal muscles, which represent the anterior myotomes of ***Amphioxus***, are arranged is shown. The tentacles of ***Amphioxus*** are represented by the tentacles of the ***Ammocœte***, the hood-like "upper lip" of the latter obviously answering to the median prolongation of the head of ***Amphioxus*** with the two lateral folds of integument which lie outside the bases of the tentacles and are continued back into the ventro-lateral ridges. The relative shortening of the notochord, and lengthening of that region of the brain which lies in front of the origins of the optic nerves, in C, as compared with B, is remarkable.

A line is drawn in all the figures through the anterior margin of the nasal sacs (*Na-Na*); another has the same relation to the eyes (*Op-Op*); and a third (*Hy-Hy*) passes through the region of the auditory sac and hyoidean arch. 1, 2, 3, hyoidean and first and second branchial clefts of ***Ammocœtes***; I., II., III., IV., &c., myotomes of ***Amphioxus***; ***My***, myelon or spinal cord; ***Ch***, notochord.

IV

ON THE BEARING OF THE DISTRIBUTION OF THE PORTIO DURA UPON THE MORPHOLOGY OF THE SKULL.

Proceedings of the Cambridge Philosophical Society, vol. ii., 1876, *pp.* 348–351.
(*Read May* 11*th*, 1874.)

IN the first place the distribution of the seventh nerve or *portio dura* in Man was compared with that of the same nerve in the *amphibia;* and it was shown that, while the proper facial nerve, with the *chorda tympani*, corresponds in all essential respects with the posterior division of the seventh nerve in the Frog and other amphibia, the *nervus petrosus superficialis major* or vidian nerve, with its palatine branches and the nerve of Cotunnius, answers to the anterior division of the seventh, or so-called "palatine" nerve of the Frog. A branch which, in the *Urodela*, connects the *portio dura* with the Gasserian ganglion, appears to be the homologue of the *nervus petrosus superficialis minor.* The tympano-Eustachian passage, in both Man and the Frog, is included between the two main divisions of the *portio dura.*—The distribution of the seventh nerve in the Ray was next described. Its two divisions were shown to have the same relation to the spiracle as they have to the tympano-Eustachian passage in the higher vertebrata. The anterior division, however, differed from that of the Frog and that of Man, in possessing no branch comparable to the nerve of Cotunnius. The place of this nerve appears to be taken by a large "palato-nasal" branch of the fifth (as Bonadorff has already suggested), and it was suggested that the Cotunnian branches of the palatine nerves in the Frog and in Man really belong to the Trigeminal. The distribution of the *portio dura* was then compared with that of the glossopharyngeal and that

of the branchial branches of the vagus, and the conclusion was drawn, that the *portio dura* is the nerve of the mandibulo-hyoid cleft (commonly called the first visceral cleft), and is distributed to the (morphologically) anterior and posterior walls of that cleft. As a corollary from this conclusion, it followed that the pterygoid arcade does not represent an independent visceral arch, but is a dependence of the mandibular arch, as Gegenbaur has already argued upon other grounds. It was further shown that the distribution of the second and third divisions of the fifth nerve is such as accords with the view that they represent the posterior division of the nerve of the trabeculo-mandibular cleft. The anterior division of that nerve was sought in the palato-nasal branch of the trigeminal—while the first division of the latter nerve appears to be the nerve of the (morphologically) anterior face of the trabecular. The sixth, third, and fourth nerves were regarded as special branches of the nerves of the mandibulo-hyoid, and trabeculo-mandibular clefts respectively, developed in relation with the special muscles of the eye. The author finally endeavoured to show that the results thus obtained by the thorough investigation and comparison of the distribution of the cranial nerves were in entire accordance with those obtained by the study of development, and that the apparent anomalies in the distribution of the fifth and of the seventh nerves in the higher *vertebrata* are easily explained by the metamorphoses of the trabecular and mandibular and hyoidean arches in these animals.

Professor HUMPHRY expressed his thanks and the thanks of those present to Prof. Huxley for the careful and lucid account which he had given of a difficult piece of anatomy, and for the interesting and morphological inferences which he had deduced from them, and also for the illustration he had given of the fact that the dullest, most troublesome anatomical details may be brightened, and so rendered easy by an insight into their true meaning. This was really the way to study anatomy, viz. to regard the various facts in connection with other facts, and so as the bases of scientific deductions. Prof. Humphry was glad to hear the nerves thus made the exponent of cranial morphology, for he had attempted the same thing many years ago in a paper read at the British Association at Leeds, when he endeavoured to show that the fore limb was not, as supposed by Prof Owen, an appendage to the skull, but formed independently from it. He then showed, from a consideration of the distribution of the cranial nerves, that the hyoid and not the scapula is the visceral arch of the occipital, and that the mandibular, the pterygo-maxillary and the ethmo-vomerine arches are the respective visceral arches of the

post-sphenoidal, the pre-sphenoidal, and the ethmoidal parts of the skull. This view he believed to be in the main correct. The nerves respectively supplied to them are the ninth and the three divisions of the fifth. Each of the latter is very closely confined to its particular visceral arch, sending a special nerve to each bone of its arch, or nearly so, whereas the seventh pair of nerves is more promiscuous in its distribution, being supplied to muscles disposed upon all the four visceral arches and having connecting links with the spinal nerves of those arches. It was to the orderly disposition of these connective links in relation to the visceral arches that Professor Huxley had now called their attention. Professor Humphry remarked that the communication between different nerves, which is a means of establishing the harmonious action of the several muscles supplied by them, was effected in three ways. *First*, by junction of their terminal branches. This is most common in the lower animals. *Secondly*, by plexuses near their origin from the brain and spinal cord, which are found, to some extent, in the lower animals, but which are more numerous in the higher animals. *Thirdly*, by means of ganglia. This last, which may be regarded as the most perfect method, is almost confined to the higher animals. Accordingly the communicating branches between the seventh and fifth, which formed the subject of the author's paper, pass to Meckel's ganglion, the otic ganglion, and the submaxillary ganglion in Mammals ; whereas in Batrachians they do not pass to these ganglions, but their junctions are effected among the terminal ramifications of the nerves. He could not agree with Prof. Huxley that the fore part of the skull was not, like the hinder part, composed of vertebral elements. It was transversely segmented after the manner of the rest of the skeleton, and these segments are vertebræ, whether the notochord exists at the part or not; and whether the segmentation takes place early or not, that is, in the cartilage or in the osseous nuclei developed in the cartilage, makes little difference. Sooner or later, in the higher animals at any rate, the segmentation occurs. The foremost elements derived from the trabeculæ had been designated as ribs by Prof. Huxley : and if they are so, they are components of those segments, of which the vertebræ form the mesial elements. He could not quite accept the view of the homologies of the mandibular arch which had been given ; but time failed to discuss these questions more fully. He concluded by again thanking Professor Huxley for this interesting communication.

V

ON THE CLASSIFICATION OF THE ANIMAL KINGDOM

The Journal of the Linnean Society. Zoology. Vol. xii., 1876, *pp. 199–226.*
(*Read December 3rd*, 1874.)

IN the twelfth edition of the 'Systema Naturæ' Linnæus gives the following definition of the object of classification:—

"Methodus, anima scientiæ, indigitat primo intuitu, quodcunque corpus naturale, ut hoc corpus dicat proprium suum nomen, et hoc nomen quæcumque de nominato corpore beneficio seculi innotuere, ut sic in summa confusione rerum apparenti, summus conspiciatur Naturæ ordo" (*l. c.* p. 13).

While entertaining the same general conception of classificatory method, Cuvier saw the importance of an exhaustive analysis of the adult structure of animals. The most complete investigation of the kind ever made under the direction of a single mind, and far surpassing all previous attempts in extent and thoroughness, is contained in the 'Leçons d'Anatomie Comparée' and the 'Règne Animal.' Cuvier's classification is purely morphological; it is an attempt to enunciate the facts of structure determined in his time, and largely by his own efforts, in a series of propositions of which the most general are the definitions of the largest groups, and are connected by a series of subordinate, differential propositions with those which constitute the definition of the species.

In his great work, the 'Entwickelungs-Geschichte der Thiere,' Von Baer, among other contributions to science of first-rate importance, showed that our knowledge of an animal's true structure must be imperfect, unless we are acquainted with those developmental stages (which are successive structural conditions) through which the animal has passed in its way from the ovum to the adult state; and,

since 1828, no philosophical naturalist has neglected embryological data in forming a classification.

In 1859, Darwin, in the 'Origin of Species,' laid a new and firm foundation for the theory of the evolution of living beings, which had been hypothetically sketched out by Lamarck, and thereby introduced a new element into Taxonomy. If a species, like an individual, is the product of a process of development, the character of that process must be taken into account when we attempt to determine its likeness or unlikeness to other species; and Phylogeny, or the history of the evolution of the species, becomes no less important an element than Embryogeny in the determination of the systematic place of an animal. The logical value of phylogeny, therefore, is unquestionable; but the misfortune is, that we have so little real knowledge of the phylogeny even of small groups, while of that of the larger groups of animals we are absolutely ignorant. To my mind there is full and satisfactory proof of the derivation of *Equus* from *Hipparion*, and of this from an Anchitherioid ancestor; and there is much to be said in favour of the derivation of other genera of existing Mammals from their Tertiary predecessors. There are also pretty clear indications of the series of changes by which the Ornithic arose out of the Reptilian type, and the Amphibian from the Fish; but I do not know that as much can be said of other large groups. We are reduced to speculation—to the formation of more or less probable hypotheses; and, though I believe that phylogenetic speculations are of great interest and importance, and are to be reckoned among the most valuable suggestors of, and guides to, investigation, I think it is well to recollect, not only that they are at present, for the most part, incapable of being submitted to any objective test, but that they are likely long to remain in that condition. For the ultimate test of the truth of a phylogenetic hypothesis is the historic record of the succession of living forms contained in the fossiliferous rocks; and the present state of geology gives no encouragement to the supposition that even the whole series of fossiliferous rocks represents a period co-extensive with the existence of life on the earth. In speculating on these subjects, it is constantly needful to remind one's self, even now, that there is every reason to believe that all the leading modifications of animal form were existent at least as early as the close of the Palæozoic epoch; and though it is true that the fossiliferous Palæozoic rocks are thicker than all the rest put together, yet the amount of progress in evolution from a moner to the fully

differentiated Vertebrata of the Trias bears an enormously larger ratio to the amount of progress from the Triassic vertebrates to those of the present day. All such comparative measurements as these are but rough aids to the imagination; but the Invertebrata yield even stronger evidence in the same direction. The larger divisions of the Arthropoda were completely differentiated in the Carboniferous epoch; so were those of the Mollusks and those of the Echinoderms. The great desideratum is the discovery of estuarine and freshwater formations of Silurian, Cambrian, and Laurentian date. At the present moment I do not think that any one is in a position to form even a probable guess as to what will be found in such deposits.

Taxonomy should be a precise and logical arrangement of verifiable facts; and there is no little danger of throwing science into confusion if the taxonomist allows himself to be influenced by merely speculative considerations. The present essay is an attempt to set a good example, and, without reference to phylogeny, to draw up a classification of the animal kingdom, which, as a fair statement of what, at present, appear to be well-established facts, may have some chance of permanence, in principle, if not in detail, while the successive phylogenetic schemes come and go. No doubt the increase of our knowledge of embryology will largely modify any conclusions which may be based upon our present imperfect acquaintance with the facts of development; and, in many cases, it is impossible to do more than suggest the conclusions towards which these incomplete data tend.

Among those animals which are lowest in the scale of organization there is a large assemblage, which either present no differentiation of the protoplasm of the body into structural elements; or, if they possess one or more nuclei, or even exhibit distinct cells, these cells do not become metamorphosed into tissues—are not histogenetic. In all other animals, the first stage of development is the differentiation of the vitellus into division-masses, or *blastomeres*, which become converted into cells, and are eventually metamorphosed into the elements of the tissues. For the former the name PROTOZOA may be retained; the latter are coextensive with the METAZOA of Haeckel.

I. THE PROTOZOA.

The movements of the body are affected either by pseudopodia or by cilia, which latter may either be small and numerous, or long and single, and at most two. When pseudopodia are the only

instruments of progression, the animal may be termed a *myxopod*; when numerous cilia, a *trichopod*; when single or double flagelliform cilia, a *mastigopod*.

Among the Protozoa, two groups are distinguishable:—1. The *Monera*; 2. The *Endoplastica*.

1. *The Monera*.—There is no "nucleus." Our knowledge of these forms and of their relations is largely due to Haeckel, who has shown that several of them present a remarkable alternation of conditions. Thus, *Protamœba* is a myxopod which may become encysted, and, in that condition, divides into several portions which are set free and resemble the parent, or are myxopods. *Protomonas* is a *mastigopod* which becomes encysted, divides, and gives rise to myxopods, which subsequently become converted into mastigopods. *Myxastrum* is a myxopod which becomes encysted, divides, and the products of division become enclosed in ovoid cases, whence they emerge as myxopods. *Vampyrella* is a myxopod which devours *Gomphonema* and other stalked Diatoms, encysts itself on their stalks, divides, and gives rise to new myxopods. In *Protomyxa*, the primitively independent myxopods unite into plasmodia. Although our knowledge of the structure of the soft parts of the *Foraminifera* is imperfect, and the case of *Gromia* suggests caution in assuming that they are all devoid of nuclei, it is probable that the great majority of the Foraminifera resemble *Protogenes* and belong to this division, the extent of which will doubtless be greatly enlarged by the discovery of new forms.

2. The *Endoplastica*.—The application of the term "nucleus" to the structure commonly so called in this division of the Protozoa, to a certain extent implies a belief in its being homologous with the histological element to which the same name is applied; and I prefer to revive a term I once proposed for the latter, and to call the body at present in question "endoplast." It may or may not be the homologue of the histological nucleus; and without expressing any definite opinion on that subject, I wish to leave it open for further consideration.

It is remarkable that among these Endoplastica there is a series of forms which run parallel with the Monera. Thus *Amœba* is like a *Protamœba* with a nucleus and, commonly, a contractile vesicle. The Infusoria Flagellata are comparable to *Protomonas* with the same additions, and attaining a considerable degree of complexity in *Noctiluca*.

The Gregarinidæ repeat the series of forms of *Myxastrum*, though some become divided into several segments, and, as E. Van Beneden has shown, acquire muscular fibres.

The Acinetidæ and the Radiolaria apparently have their moneral representative in *Actinophrys sol*, though the conversion of the pseudopodia into suckers in the Acinetidæ distinguishes them remarkably.

On the other hand, while no moneral trichopod seems yet to have been discovered, the trichopod type is richly represented, in this division, by the Catallacta of Haeckel, and by the Infusoria Ciliata, of which I think the Catallacta should form only a subdivision.

It is among the Ciliata that the Endoplastica attain their greatest degree of complexity, by a process of direct differentiation of their protoplasmic substance into tissues and organs, without the intervention of cell-formation.

I have recently examined several genera of Infusoria (*Paramecium*, *Balantidium*, *Nyctotherus*, *Spirostomum*) with great care—using very high microscopic powers (1,200–2,000 diameters), employing osmic acid (which at once kills and preserves unchanged the tissues of the Infusoria) and other reagents, and comparing them with such truly cellular organisms of similar size as *Opalina*, and I must express my entire agreement with Von Siebold and with Haeckel in their conclusion, that the protoplasm of these animals is not differentiated into cells.

At most there is an excessively minute, and sometimes regular, granular structure, which is found in the endoplast as well as elsewhere, and appears to me to be altogether similar to that of the protoplasm between the nuclei of *Opalina*. But although the bodies of the Infusoria contain no cells, they may be differentiated into very definite tissues. In the genera mentioned, the so-called "cuticula" is, I believe, simply the transparent outermost layer of the protoplasm, and the cilia are directly continuous with it. Beneath this is a well-marked cortical layer, in which the "trichocysts" of *Paramecium* are situated, and which, in *Spirostomum*, *Balantidium*, and *Nyctotherus*, presents the distinct muscular fibres described by Stein and others. The inner substance is, in some (*Balantidium*, *e. g.*), semi-fluid, and undergoes an obvious rotation ; but in *Nyctotherus*, not only is there no movement of this substance, but the long curved œsophagus is succeeded by an ill-defined region, which lies between it and the anus, is permanently filled with ingested matter, and is, in one sense, an alimentary tract. Even in *Paramecium*, the complex water-vessels, which lie, for the most part, not in the cortical layer, but beneath it, show, by the permanence of their disposition, that a great part of the inner substance is fixed. The constancy of position of the endo-

plast,[1] which also lies beneath, and not in, the cortical layer, is evidence to the same effect.

In comparing the Ciliated Infusoria with nucleated cells, the existence of the so-called "nucleolus," which assuredly can have nothing to do with the histological element so named, and which I propose to term the *endoplastula*, is an important fact, often left out of sight.

I have no observation to offer upon the vexed question of the nature of the endoplastula, as none of the numerous individuals of the different species named, which I have examined, showed the changes described by so many observers. That the endoplast itself is a reproductive organ is clear; but the development of embryos by its fission is an argument rather against, than in favour of, identifying it with the nucleus of a cell. No cell is known to multiply by fission of its nucleus alone.

On the whole, while I hesitate to absolutely identify the endoplast of an Infusorian with the nucleus of a histological cell, and can find no analogue for the endoplastula in the latter, I think that Von Siebold's view holds good, and that the higher Infusoria are unicellular animals, in the sense that *Mucor*, *Vaucheria*, and *Caulerpa* are unicellular plants.

Nevertheless it must be admitted, on the other hand, that though the view for which Ehrenberg has so long contended, that the *Infusoria* possess, in miniature, an organization, in a broad sense, as complex as that of the higher animals, is not tenable, the great majority of them are far more highly organized than was suspected before that indefatigable observer commenced his long and remarkable series of investigations.

II. The Metazoa.

The germ undergoes differentiation into histogenetic cells; and these cells become arranged into two sets, the one constituting the outer wall of the body, while the other lies internal to the foregoing, and forms the lining of the alimentary cavity, when, as is usually the case, a distinct alimentary cavity exists. In the embryo, the representatives of these two layers are the *epiblast* and *hypoblast*. In the adult, they are the *ectoderm* and the *endoderm*, which answer to the *epidermis*, and the *epithelium* of the alimentary canal, in the higher animals.

All the Metazoa, in fact, commence their existence in the form of

[1] The membranous investment of the endoplast, so often described and figured, certainly has no existence in the unaltered state of the Infusoria I have mentioned.

an ovum, which is essentially a nucleated cell, supplemented by more or less nutritive material, or *food-yelk*. The ovum, after impregnation, divides into blastomeres, giving rise to a *Morula* (Haeckel), in the midst of which arises a cavity, the *blastocœle* (*cleavage-cavity*, "*Furchungshöhle*" of the Germans), which may be larger or smaller, filled only with fliud, or occupied by food-yelk. When it is largest, the blastomeres, united into a single layer, form a spheroidal vesicle, enclosing a correspondingly shaped blastocœle. When it is reduced to a minimum, the *Morula* is an almost solid aggregation of blastomeres, which may be nearly equal in size, or some much larger than others, in consequence of having undergone less rapid division. The next stage in the development of the embryo of a Metazoon consists (in all cases except a few parasitic anenterous forms) in the conversion of the *Morula* into a body having a digestive cavity or a *Gastrula*. The conversion of the *Morula* into the *Gastrula* may take place in several ways.

In the simplest, the *Morula*, being composed of equal or nearly equal blastomeres, these, undergoing conversion into cells, differentiate themselves into an epiblast, which invests the remaining cells, constituting the hypoblast. The central cells of the hypoblast next diverge and leave a space filled with fluid, the alimentary cavity, which opens at one end, and thus gives rise to the *Gastrula*. This is the process generally observed in Porifera, Cœlenterata, Turbellaria, Trematoda, and Nematoidea.

In a second class of cases, the *Morula* becomes converted into blastomeres of unequal sizes, a small and a large set. The smaller are rapidly metamorphosed into cells, and invest the larger (with any remains of the food-yelk) as a blastoderm. The hypoblast arises either from the blastoderm thus formed, or from the subjacent larger blastomeres. This is the process observed in certain Turbellaria, in the Ctenophora, in most of the Oligochæta and Hirudinea, in the Arthropoda, and in most Vertebrata.

In a third group of instances, the *Morula*, whether consisting of equal or unequal blastomeres, becomes spheroidal, and encloses a correspondingly shaped blastocœle. One part of the wall of this vesicular *Morula* then becomes invaginated, and is converted into the hypoblast, which encloses the alimentary cavity, the latter communicating with the exterior by the aperture of invagination. This process has been observed in the Chætognatha, Echinodermata, and some Gephyrea, in *Lumbricus* and *Hirudo*—in polychætous Annelida, Enteropneusta, Brachiopoda, and most Mollusca—and in *Amphioxus*, *Petromyzon*, and the Amphibia among the Vertebrata.

The various modes in which the two primary layers of the germ may be developed shade off into one another, and do not affect the essence of the process, which is the segregation of one set of cells to form the external covering of the body, and of another to constitute the lining of the alimentary canal. We may, with Haeckel, term those animals which pass through the Gastrula stage, *Gastreæ*. The *Gastrula* may be deeply cup-shaped, or flattened out into a disk, slightly concave on one side; but in whatever manner the *Gastrula* is formed, and whatever be its shape when its alimentary cavity is complete, one of two things happens to it. It becomes provided with many ingestive apertures distinct from that first formed (polystomatous), or with one only, which may or may not be distinct from the first aperture of the *Gastrula* (monostomatous).

Metazoa polystomata.—The former division comprises only the Sponges (Porifera or Spongida), in which, as the remarkable researches of Haeckel ('Monographie der Kalk-Schwämme') have shown, the walls of the deeply cup-shaped *Gastrula* become perforated by the numerous inhalent ostioles, while the primitive opening serves as the exhalant aperture.

The latter division includes all the remaining forms, which may be grouped together as *Metazoa monostomata*. Among these, two primary groups are distinguishable, of which the second exhibits an advance in organization upon the first. In the first, the primitive aperture of the *Gastrula* becomes the permanent mouth (Archæostomata). In the second, the permanent mouth is a secondary perforation of the body-wall (Deuterostomata).

1. *The Archæostomata.*—It is now well established that the aperture of the *Gastrula* becomes the oral aperture of the adult in the Cœlenterata, which group includes animals differing much in grade of organization, from the simple *Hydra* to the complex *Ctenophore*, but all manifestly exhibiting variations of one fundamental type.

In most of the Hydrozoa, the ovum passes into a solid *Morula*, which, as in the Porifera, becomes differentiated into an epiblast and a hypoblast. The central cavity of the latter opens at one end, and thus far the *Gastrula* of the Hydrozoa is very like that of the sponges; but the aperture produced in this manner becomes the mouth; and if, as not unfrequently happens, apertures are formed elsewhere, they do not serve the purpose of taking in food. In such Hydrozoa as have thickened body-walls, hollow prolongations of the hypoblast extend into the blastocœle, and are surrounded by a mesoblastic tissue. These prolongations may become branched

and anastomose, resembling vascular canals; but they remain permanently in connection with the alimentary cavity. The reproductive elements are developed in the body wall, and usually in cæcal outwardly projecting processes of that wall, which dehisce and set free the ova and spermatozoa upon the outer surface of the body.

The Actinozoa, while presenting the same continuity of the cavity of the body with the alimentary cavity which is exhibited by the Hydrozoa, differ from them in two respects. The commencement of the alimentary canal is, as it were, sunk in the body; and the reproductive elements are developed in the walls of the gastrovascular canals, and pass into them on their way outwards.

The development of the coralligenous Actinozoa has not yet been thoroughly worked out; but Lacaze-Duthiers has shown that, in *Corallium rubrum* and other Gorgonidæ, the *Morula* passes into an elongated, almost vermiform, ciliated *Gastrula*, which becomes fixed by one end, and then develops the intermesenteric chambers. It can hardly be doubted that these are formed as diverticula from the basal end of the primitive alimentary canal, in which case the developmental process differs but little, essentially, from that of such a Hydrozoon as *Carmarina hastata*; and the line of demarcation between the Actinozoa and the Hydrozoa becomes very narrow.

The Ctenophora, on the other hand, differ somewhat in development, as in other respects, from the Coralligena. Their development has been carefully worked out by Kowalewsky, and more recently by Agassiz.

The laid egg is contained in a spacious capsule, and consists of an external thin layer of protoplasm, which, in some cases, is contractile, investing an inner vesicular substance. The vitellus thus constituted divides into two, four, and, finally, eight masses; on one face of each of these the protoplasm-layer accumulates, and is divided off as a blastomere of much smaller size than that from which it arises. By repeated division, each of these gives rise to smaller blastomeres, which become nucleated when they have reached the number of 32, and form a layer of cells, which gradually spreads round the large blastomeres, and invests them in a complete blastodermic sac. At the pole of this sac, on the face opposite to that on which these blastoderm-cells begin to make their appearance, an ingrowth or involution of the blastoderm takes place, which, extending through the middle of the large yelk-masses towards the opposite pole, gives rise to the alimentary canal. This, at first, ends by a rounded blind termination; but from it, at a later period, prolongations are given off, which become the gastro-vascular canals.

At the opposite pole, in the centre of the region corresponding with that in which the blastoderm-cells first make their appearance, the nervous ganglion is developed by metamorphosis of some of these cells.

It is clear that the invaginated portion of the blastoderm, which gives rise to the alimentary canal, answers to the hypoblast, while the rest corresponds with the epiblast.

The large blastomeres which become enclosed between the epiblast and hypoblast in the manner described, appear to serve the purpose of a food-yelk; and the space which they originally occupied is eventually filled by a gelatinous connective tissue, which possibly derives its origin from wandering cells of the epiblast.

The Actinozoa and the Hydrozoa constitute the Cœlenterata, which are definitively characterised by the fact that, in all the higher forms, the mesoblast is traversed by canals formed by diverticula of the hypoblast, which permanently remain in continuity with the alimentary cavity, and that, in the lower forms, the alimentary cavity is prolonged into the cœnosarc. They are usually said to have a radiate symmetry; but even in the *Actiniæ*, there are traces of bilaterality; and in the Ctenophora, the bilateral symmetry of the adult is obvious.

Parallel with these may be ranged an assemblage composed of the Turbellaria, Rotifera, and Trematoda, the Nematoidea, Oligochæta, and Hirudinea, to which the name of 'Scolecimorpha' may be applied. They are associated together by the closest resemblances of structure, and present an even greater range in grade of organization than the Cœlenterata. The lower Rhabdocœla come very close to the Infusoria (as close as the multicellular to the unicellular Algæ), and are but little superior to *Hydra* in the degree of their organic differentiation, while in the land-Planariæ, the Trematoda, and the Nemertidæ we have animals which attain a considerable complexity and, in the case of many Trematoda and of *Lineus* (*Pilidium*), undergo remarkable metamorphoses. Such forms as *Dinophilus* appear to connect the rhabdocœle Turbellaria with the Rotifera. The lower Nematoidea are extremely simple, while the higher are considerably differentiated; and, as Schneider has shown, they are connected with the Turbellaria by such forms as *Polygordius*. The Oligochæta and the Hirudinea either belong to this division, or constitute a transitional group between it and the Deuterostomata. In *Lumbricus* (and apparently in *Hirudo*) there seems to be no doubt that the aperture of invagination of the *Gastrula* becomes the mouth. According to Kowalewsky, the mouth in *Euaxes* and *Tubifex* is of

secondary origin; but its close resemblance to that of the earthworm and of the leech embryos leads me to suspect that there must be some error of interpretation here. On the other hand, it may be that these are transitional forms, such as we may expect to find bridging over the intervals between all groups, as knowledge widens. In any case they differ from the foregoing in the development of a segmented mesoblast. In the Cœlenterata, Nematoidea, Turbellaria, Trematoda, and Rotifera, the mode of origin of the cells which lie between the epiblast and the hypoblast, constitute the mesoblast, and give rise to the connective tissues and muscles of the body-wall and of that of the intestine, is not precisely known. They may take their origin in the epiblast or in the hypoblast, or in both. But in the Earthworm and Leech, after the epiblast and hypoblast are differentiated, the cells of the latter give rise, by division, to two bands of cells which lie one on each side of the long axis of the ventral face of the worm, and constitute the mesoblast. This becomes marked out by transverse constrictions into segments, and in each segment gives rise to all the tissues which lie between the epiblast and hypoblast. The mouth corresponds with the primitive involution of the *Morula*; the anal aperture is a new formation.

In the Nematoidea and in the lower rhabdocœle Turbellaria, the intestinal canal is a simple tube or sac. But, in some Turbellaria and Trematoda the alimentary canal gives off diverticula, which ramify through the mesoblast and even unite together, giving rise to a gastrovascular canal system like that of the Cœlenterata. These animals, therefore, have what may be termed an *enterocœle*, more or less distinct from the proper digestive cavity, but connected with it, ramifying through the mesoblast.

Whether the remarkable group of worms termed Gephyrea by De Quatrefages (and including *Sipunculus*, *Sternaspis*, *Bonellia*, &c.) belong to the Archæostomata, or not, is uncertain, too little being known of the early stages of their development. They appear to me to be closely allied to the Rotifera (compare *Bonellia*, for example) to the Enteropneusta and to the Echinodermata; while Schneider, by his very ingenious comparison of the *Phoronis*-larva *Actinotrocha* with *Cyphonautes*, affords even stronger grounds than those furnished by the structure of *Phoronis* itself, for suspecting that the Gephyrea and the Polyzoa are more intimately connected than has been supposed to be the case.

It will be observed that the Scolecimorpha present a series of modifications from the unsegmented Turbellaria and Nematoidea, through the imperfectly segmented Rotifera, to the polymerous

Oligochæta and Hirudinea, and that the segmentation primarily occurs in the mesoblast.

2. The *Deuterostomata.*—In the remaining Gastreæ the embryo develops a secondary mouth as a perforation of the body-wall, the primary aperture sometimes becoming the anus and sometimes disappearing.

The *Schizocœla.*—Of these Metazoa Deuterostomata there are some which follow the mode of development of the Oligochæta and Hirudinea very closely, so far as the formation and segmentation of the mesoblast is concerned; though the question whether this segmented mesoblast arises from the epiblast or the hypoblast, has not been exhaustively worked out. These are the Annelida Polychæta.

It is a very general, if not universal, rule among these animals, that the *Gastrula* is formed by invagination, and that the aperture of invagination persists as the anus of the adult. Almost universally, again, the outer surface of the *Gastrula* is provided with cilia, by the working of which it is actively propelled through the water in which it lives; and these cilia usually become restricted to certain areas of the body, in the form of zones transverse to its long diameter. In this respect the larvæ of some Gephyrea present similar features. Moreover setæ, developed in involutions of the ectoderm, are very generally present, especially on the limbs, when such exist. Some are apodal; some possess symmetrically disposed setæ in each segment of the body; and in many, true though rudimentary limbs (*parapodia*), one pair for each segment of the body, occur. In a few of the highest forms (e.g. *Polynoë*) some of the anterior limbs are turned forwards, and lie at the sides of the mouth, foreshadowing the jaws of the Arthropoda. In some, a process of the ectoderm, in the region of the head gives rise to a cephalic hood or mantle. A perivisceral cavity occupies the space between the wall of the body and that of the alimentary canal, and, so far as is known, is invariably formed in the substance of the mesoblast, by a sort of splitting or divarication of its constituent cells, whence it would seem to be a rehabilitation of the primitive blastocœle. The great majority of the *Polychæta* possess the so-called "segmental organs"—variously formed tubes, which open on the surface of the body, on the one hand, and, usually, into the perivisceral cavity on the other. Not unfrequently these, or some of them, play the part of conduits of the generative products.

The lower Arthropoda closely resemble the Polychæta in their development, except that the food-yelk is usually large, the ali-

mentary cavity is rarely formed by invagination, and cilia are never met with in any part of the body.[1] The mesoblast is developed and becomes segmented precisely in the same way. Limbs are formed and rarely remain rudimentary; usually they become jointed; and, in almost all cases, more or fewer of those which lie in the neighbourhood of the mouth are converted into jaws. The perivisceral cavity is formed in the same way as in the foregoing group; so that the Arthropoda, like the Polychæta, are "schizocœlous." In the higher Insecta, the embryogenetic process is complicated by the development of an amnion, which singularly resembles that met with in the higher Vertebrata. Mr. Moseley's recently published careful examination of *Peripatus* tends to show that this animal, formerly regarded as an Annelid, is really a low and primitive form of Arthropod, and thus affords evidence of the highest significance as to the relations of the Annelida with the Arthropoda.

The true position of the Polyzoa is as yet, as I have already said, a matter of doubt; but the arguments of Morse, and still more the recent investigation of Kowalewsky into the development of the Brachiopoda, place the close affinity of the latter with the Annclida in a clear light. The free larva of *Argiope*, for example, is wonderfully similar to those of *Spio* and of *Spirorbis*; and the mantle of the Brachiopoda appears to correspond with the cephalic hood of these Annelids. When it first becomes fixed, on the other hand the young Brachiopod has many resemblances to *Loxomma* and *Pedicellin* among the Polyzoa.

As regards the Mollusca proper,[2] the larvæ of the Lamellibranchiata, and of the majority of the Odontophora, have their parallel in the larva of the Annelidan *Phyllodoce*, while the young of *Dentalium* and of the Pteropods correspond with the larvæ of other Annelids. A Mollusk appears to me to be essentially an Annelid which is only dimerous, or trimerous, instead of polymerous.

The development of the perivisceral cavity in the Molluscan series, stands much in need of elucidation. There seems to be little reason to doubt that the higher Mollusks are Schizocœlous; but it is possible that the lower forms are Enterocœlous, like the members of the next division.[3]

[1] The like absence of cilia is a notable peculiarity of *Hirudo*, among the Leeches.

[2] See Mr. Lankester's valuable paper "On the Development of *Lymnæus*," Quarterly Journal of Microscopical Science.

[3] When I wrote this paragraph, I had been for some time in possession of the recent important memoir on the development of the Brachiopoda by M. Kowalewsky, as that distinguished embryologist had been good enough to send it to me. But it is written in Russian,

The *Enterocœla*.—Kowalewsky has shown that in the Chætognatha, represented by the strange and apparently anomalous *Sagitta*, the vitellus undergoes complete segmentation, and is converted into a vesicular *Morula*, on one side of which invagination takes place, and gives rise to the primitive alimentary canal, of which the opening of invagination becomes the permanent anus, the mouth being formed, by perforation, at the opposite end of the body. Before the mouth is formed, however, the primitive alimentary cavity throws out, on each side, a cæcal pouch, which extends as far forward as its central continuation ; while posteriorly these pouches stretch behind the anus, meeting, but remaining separated by their applied walls, in the median plane of the body. These lateral sacs are next shut off from the median portion of the primitive alimentary cavity, which becomes the permanent alimentary canal ; and they are converted into closed sacs, the cavity of each of which forms one half of the perivisceral cavity, while the inner wall, applied to the hypoblast, gives rise to the muscular wall of the intestine, and the outer wall, applied to the epiblast, becomes the muscular wall of the body, and gives rise to the generative organs. The great ganglia and nerves are developed from the cells of the epiblast. We have thus an animal which is temporarily cœlenterate, but in which the two gastrovascular sacs, enclosing what may be termed an "enterocœle," become shut off and metamorphosed into parts of exactly the same order as those which arise from the mesoblast of an Annelid. But it is not altogether clear whether the cells of the enterocœle in this case give rise only to the lining of the perivisceral cavity, and whether the muscles and connective tissue are in fact derived from the epiblast or not. Kowalewsky's evidence, however, is in favour of the origin of the muscles directly from the cells of the mesoblastic diverticula.

The brilliant investigations of Johannes Müller upon the development of the Echinodermata, confirmed in their general features by all subsequent observers, have proved, first, that the ciliated embryonic *Gastræa* (the primitive alimentary canal of which is formed by involution of a vesicular blastoderm), to which the egg of all ordinary Echinoderms gives rise, acquires a mouth by the formation

and I could only judge from the figures that the perivisceral cavity of *Argiope* is developed in the same way as that of *Sagitta*. Some little time ago, however, my friend Mr. W. F. Ralston kindly took the trouble to translate so much of the text as referred to these figures for me, and I found that my interpretation of them was correct. The Branchiopoda, or some of them, therefore, are Enterocœla; and their relations with the schizocœle Annelida and Mollusca bring up anew the question suggested by the frequent origin of the mesoblast from the hypoblast (as in the Sharks, for example). May not the schizocœle be derivable from a primitive enterocœle condition?

of an aperture in the body-wall distinct from the primitive aperture of the *Gastræa*, so that, in this respect, it differs from all Cœlenterata; secondly, that the embryo thus provided with mouth, stomach, intestine, and anus acquires a completely bilateral symmetry; thirdly, that the cilia with which it is primitively covered become restricted to one or more circlets, some of which encircle the axis of the body, or a line drawn from the oral to the anal apertures; and, fourthly, that within this bilaterally symmetrical larva or *Echinopædium*, as it may be called, the more or less completely radiate Echinoderm is developed by a process of internal modification.

Müller believed that the first step in this process was the ingrowth of a diverticulum of the integument, as a hollow process, out of which the ambulacral vascular system of the Echinoderm took its rise. He did not attempt to explain the origin of the so-called blood-vascular system (or pseudhæmal vessels), nor of the perivisceral cavity. Müller's conclusions remained unchallenged until 1864, when Prof. Alexander Agassiz took up the question afresh, and, in a remarkable paper on the development of the genus *Asteracanthion*, detailed the observations which led him to believe that the ambulacral vessels do not arise by involution of the external integument, but that they commence as two primitively symmetrical diverticula of the stomach (the "würstformige Körper" of Müller), one of which becomes connected with the exterior by an opening (the "dorsal pore" observed by Müller, and considered by him to be the origin of the ambulacral vessels) and gives rise to the ambulacral vessels, the ambulacral region of the body of the Echinoderm being modelled upon it; while, upon the other gastric sac, the antambulacral wall of the starfish-body is similarly modelled. Both gastric sacs early become completely separated from the stomach of the *Echinopædium*, and open into one another, so as to form a single horseshoe-shaped sac connected with the exterior by a tube which is converted into the madreporic canal. Agassiz does not explain the mode of formation of the perivisceral cavity of the starfish, and has nothing to say concerning the origin of the pseudhæmal vessels.

Recently Metschnikoff has confirmed the observations of Agassiz, so far as the development of the ambulacral system from one of the diverticula of the alimentary canal of the starfish larva is concerned; and he has added the important discovery that the perivisceral cavity of the Echinoderm is the product of the rest of these diverticula. Moreover his observations on other Echinodermata show that essentially the same process of development of the peritoneal cavity occurs in Ophiuridea, Echinidea, and Holothuridea.

The precise mode of origin of the pseudhæmal system, or so-called blood-vessels, of the Echinoderms is not yet made out. But it is known that the cavity of these vessels contains corpuscles similar to those which are found in the perivisceral cavity and in the ambulacral vessels, and that all of these communicate together.

Agassiz and Metschnikoff alike justly insist upon the correspondence in development of the lateral gastric diverticula of the *Echinopædium* with that of the trunks of the gastrovascular system of the Ctenophora; and, on the ground of this resemblance, the former refers the Echinoderms to the Radiata, retaining under that Cuverian denomination the Acalephæ (Cœlenterata) and the Echinodermata. But this arrangement surely ignores the great value of his own discovery, which shows that the Echinoderms have made a great and remarkable progress in passing from their primarily cœlenterate stage of organization to their adult condition. And it further ignores the unquestionable fact, admirably brought out by the same able naturalist's investigations into the development of *Balanoglossus*, that the *Echinopædium* is almost identical in structure with the young of animals such as the Gephyrea and Enteropneusta, which are in no sense radiate, but are eminently bilaterally symmetrical. In fact, the larva of *Balanoglossus*, the sole representative of the Enteropneusta, was originally described by Müller under the name of *Tornaria*, as an Echinoderm larva, and was subsequently more fully examined by Prof. Alex. Agassiz, who also regarded it as an unquestionable Echinoderm larva; and it is only recently that it has been proved, partly by Metschnikoff and partly by Agassiz himself, to be the larval form of *Balanoglossus*. In *Balanoglossus*, as in the Echinoderms, saccular diverticula of the intestine appear to give rise to the perivisceral cavity and its walls. In the Chætognatha, Echinodermata, and Enteropneusta, therefore, the perivisceral cavity is a portion of the alimentary cavity shut off from the rest; and in contradistinction to the Schizocœla, in which the perivisceral cavity is produced by a splitting of the mesoblast, they may be said to be Enterocœla.

The *Epicœla*.—In the Ascidians, the investigations of Kowalewsky, now confirmed in all essential points by Kupffer, have shown that the alimentary cavity is formed by the invagination of the vesicular *Morula*, that the blood-channels answer to the blastocœle, that the central nervous system is produced by invagination of the epiblast, as in the Vertebrata, and that, in most, the mesoblast of a caudal prolongation gives rise to an axial column flanked by paired

myotomes, which are comparable to the notochord and myotomes of the vertebrate embryo.[1]

In the simplest Ascidians (the *Appendicularia*) the modified pharynx, which constitutes the branchial sac, is perforated by only two apertures, which open on the hæmal or ventral face of the body, and there is no atrial chamber. But in all other Ascidians an invagination of the epiblast takes place on each side of the anus, and, extending alongside the branchial sac nearly as far as the endostyle, give rise to a spacious chamber, lined by the so-called atrial or "third" tunic. In many Ascidians the chamber extends much further, so that even the alimentary canal and the generative organs are situated between the atrial tunic and the ectoderm. In this manner a kind of "perivisceral cavity" is formed, which is of a totally different nature from the "schizocœle" of the Annelid, and from the "enterocœle" of the Echinoderm, and which may be termed an epicœle.

The resemblance of the simplest of vertebrated animals, the Lancelet (*Amphioxus lanceolatus*), to the Tunicata was first indicated, though, it must be admitted, very vaguely, by Goodsir.[2] In 1852 I gave full reasons for believing that the branchial sac of the Ascidian "represents, not the gill of the Mollusk, but the perforated pharynx of *Amphioxus*"[3]; and I described the development of the muscles of the tail in the larval Ascidian as "closely resembling that of the muscles of the Tadpole;" but in the absence

[1] It is with great diffidence that I venture to express my dissent from the views of my venerated friend Von Baer, from whose works I first gathered sound principles of morphological science, and whose authority in such a matter as this has no equal; but I cannot think that the doubts he has expressed respecting the fundamental similarity between the Ascidians and the Vertebrata are warranted.

[2] "On the Anatomy of *Amphioxus lanceolatus*." Read before the Royal Society of Edinburgh, May 3rd, 1841, and published in vol. xv. of the 'Transactions' of that Society. "Viewed as an entire animal, the Lancelet is the most aberrant in the vertebrate subkingdom. It connects the Vertebrata, not only to the Annulose animals, but also, through the medium of certain symmetrical Ascidiæ (lately described by Mr. Forbes and myself), to the Molluscs. We have only to suppose the Lancelet to have been developed from the dorsal aspect, the seat of its respiration to be transferred from the intestinal tube to a corresponding portion of its skin, and ganglia to be developed at the points of junction of one or more of its anterior spinal nerves and inferior branch of its second pair, to have a true annulose animal, with its peculiar circulation, respiration, generative organs, and nervous system, with supra-œsophageal ganglia, and dorsal ganglionic recurrent nerve."

With every desire to give credit for sagacity where it is due, I think it is obvious from this passage, and from the fact that Goodsir denied the existence of the branchial clefts, or even of the abdominal pore, in *Amphioxus*, that he had no conception of its true morphological relations, and no valid grounds for the hint which he throws out.

[3] Report of the Belfast Meeting of the British Association, 1852. Transactions of the Sections, pp. 76, 77.

of any sufficiently detailed knowledge of the development of the embryo of either the Ascidian or of *Amphioxus*, it was impossible to know what weight ought to be attached to these resemblances; and it was not until the publication of the memoir of Kowalewsky on the development of *Amphioxus* that their real significance became manifest.

In this animal, in fact, yelk-division gives rise to a vesicular *Morula*, which becomes provided with an alimentary cavity by invagination, and with a cerebrospinal axis by the development of laminæ dorsales and the invagination of the corresponding portion of the epiblast, as in other Vertebrata.

The branchial clefts are secondary perforations of the body-wall and pharynx; and the protovertebræ and notochord are developed, as in Annelids and Arthropods, out of a mesoblastic layer situated between the epiblast and hypoblast, and therefore in the blastocœle. But one of the most important points made out by Kowalewsky is, that the branchial clefts at first open externally—and that they only acquire their anomalous position in the adult by the growth over them of two laminæ of the body-wall, which unite in the median ventral line for the greater part of their length, leaving only the abdominal pore open.

Although the structure of *Amphioxus* has been investigated by many able observers [1] during the last forty years, a re-examination of this singular animal, with which I first made acquaintance in 1846, has convinced me that some of its most remarkable morphological features have hitherto escaped notice; and I will take this occasion of laying a summary of the chief results at which I have arrived before the Linnean Society.

Amphioxus has hitherto been generally assumed to be a vertebrated animal, which differs from all others in possessing a mere rudiment of brain and of skull, and in being devoid of renal organs.

It is quite true that *Amphioxus* has neither brain nor skull, if we restrict the application of these terms to those particular forms under which the brain and skull are met with in the higher Vertebrata; but if we ask whether those regions of the cerebro-spinal axis, and of the axial endoskeleton, which are metamorphosed into the brain and skull in the higher Vertebrata are, or are not, represented in *Amphioxus*, the answer must be that these regions are not only present, but that, in relation to the size of the body, they are much longer than in any

[1] I need only mention the names of Retzius, Rathke, Müller, Goodsir and Quatrefages. Within the last two years Stieda has published an elaborate paper on *Amphioxus* in the Transactions of the Academy of St. Petersburg.

other Vertebrate, and that, in this respect, as in so many others, *Amphioxus* is the counterpart of the embryo of the higher Vertebrate.

The oral aperture of *Amphioxus* is surrounded by a series of tentacula ; and the spacious buccal chamber is divided from the branchial one by a curiously arranged valvular " velum " (the " Franzen " of Müller). Close to the anterior end of the cerebro-spinal axis, is the ciliated olfactory sac discovered by Kölliker ; and the pigment-spot, which represents the eye, coats the extremity of the same part of the cerebrospinal axis.

On comparing *Amphioxus* with the Lamprey, in its larval or *Ammocœtes* condition, the cerebrospinal axis of the latter is seen to be a mere rod somewhat enlarged at its anterior end, where it bears a mass of pigment representing the eye, and connected, by a very short cord, with a single ciliated olfactory sac. The oral aperture of the *Ammocœtes* is also surrounded by tentacles ; and, as in *Amphioxus*, leads into a wide buccal cavity, which is separated from the branchial sac by two remarkable folds, originally described by Rathke, which answer to the velum of *Amphioxus*. But the dorsal ends of the attached edges of these folds are situated immediately under the middle of each auditory capsule ; and, in the adult Lamprey, they can be proved to correspond with the position of the hyoidean arch In the *Amphioxus* their dorsal attachment corresponds with the anterior angulation of the intermuscular septum between the sixth and seventh myotomes, counting from the anterior end of the body. Hence, it follows that this septum answers to the hyoidean arch of the higher Vertebrata, and that the six myotomes in front of it represent six primary segments of the body, or somatomes. But the first of these lies behind the eye, whence it also follows that the region occupied by these somatomes answers to the region included between the optic foramen and that for the seventh nerve in the skull of an ordinary vertebrated animal, and that so much of the head of *Amphioxus* as lies in front of the hyoid region answers to the præauditory moiety of the skull in other Vertebrata.

In *Amphioxus*, a nerve leaves the cerebrospinal axis in correspondence with the interval between each pair of myotomes, and then divides into a dorsal and a ventral branch, like an ordinary spinal nerve. And, in front of the first myotome, two nerves, or perhaps one nerve in two divisions, are given off. The more anterior of these two passes above the eye, and is distributed to the end of the body in front of the mouth, while the second and the other nerves pass to the side walls of the oral cavity.

These nerves, arising as they do between the homologue of the

optic nerve and that of the *portio dura*, must represent the third fourth, fifth, and sixth pairs of cranial nerves of the ordinary Vertebrata; while the myotomes between which five of them pass must represent the muscles of the nose, eye, and jaws. In fact, the course of the most anterior nerve is exactly that of the orbito-nasal nerve (the so-called ophthalmic, or first, division of the trigeminal), as is conspicuous when this nerve in *Amphioxus* is compared with the undoubted orbito-nasal of the Lamprey.

In the embryo Lamprey, at the most advanced stage described by Schulze, the portion of the centro-spinal axis which lies between the ear and the eye is relatively very long; but the cerebral hemispheres are beginning to grow out beyond the primitive anterior end of the cerebro-spinal axis, and project beyond the eye. In the young *Ammocœtes* of 1·5 inch long the length is still great, though it has not increased in proportion to the body; but the cerebral hemispheres are relatively larger, and the eyes are fully formed and have moved backwards, dividing the series of myotomes into a supraocular and a subocular bundle of muscles. And, in the adult Lamprey, changes in the same direction have gone still further.

It is clear, therefore, that the region occupied by the six most anterior myotomes of the body of *Amphioxus* answers to the præauditory region of the skull in the higher Vertebrata. The question next arises, how many of the succeeding myotomes are included in the region which corresponds with the postauditory or parachordal region of the skull in the higher Vertebrates?

The Lamprey has seven branchial sacs, with as many external clefts; and no Vertebrate ever possesses more. To each of these sacs nerves pass which undoubtedly correspond with the branchial branches of the glossopharyngeal and pneumogastric nerves; and strong grounds for thinking that the pneumogastric trunk contains the representatives of, at fewest, six primary distinct nerves, answering to the six posterior branchial sacs, have been given by Gegenbaur and myself. If this be so, then the seven pairs of nerves behind the representative of the portio dura in *Amphioxus* will answer to the glossopharyngeal and pneumogastric, and the eighth somatome will correspond with the occipital segment of the Ichthyopsida. Thus the skull of a Lamprey or of an Elasmobranch fish is represented by the anterior region of the body of the *Amphioxus* as far back as the fourteenth myotome. As there are from sixty to seventy myotomes, this estimate makes the head of *Amphioxus* to occupy, morphologically, one fifth of the whole body.

With respect to the renal organs, Müller thought he had observed

some rounded bodies which might have a renal character in the posterior part of the abdominal cavity of living specimens of *Amphioxus*; but as he could not find them by dissection, and as no other anatomist has been more successful, they need not now be discussed.

Rathke described two canals situated in the ridges which are developed at the junction of the ventral with the lateral faces of the body. He states that these canals open, behind, at the abdominal pore, and in front at the mouth. Müller and, more recently, Stieda confirm Rathke's account, which appeared to be strengthened by Kowalewsky's statement that he had seen the ova pass out by the mouth. Nevertheless there are no such canals. The ventro-lateral folds in question begin on each side of the front part of the mouth, and are continued alongside it, as Goodsir rightly states, becoming deeper as they pass back. At the sides of the abdominal pore, they terminate without uniting, one on each side of the præanal fin. In the living state, as well as in spirit specimens, these ventro-lateral laminæ are strongly curved inwards; and they meet, or nearly meet, in the middle line, more or less covering the proper ventral aspect of the body, between the mouth and the respiratory pore. And it is simply the semicanals enclosed by these infolded ventro-lateral laminæ which Rathke took for abdominal canals, open only in front and behind. The superficial layer of the integument, with its epiderm, is continued from the outer margin of each ventro-lateral lamina, over its edge, on to the inner surface of the lamina, and, in the normal state, is closely adherent to the greater part of that surface, becoming detached, to be reflected on to the proper ventral face of the body, only at the re-entering angle between the ventro-lateral lamina and the ventral face. But, in spirit specimens, this superficial layer, which coats the inner face of the ventro-lateral lamina, sometimes becomes detached, along with more or less of its continuation on to the ventral surface of the body, and leaves a wide space, which is the abdominal canal described by Stieda, and erroneously supposed by him to be Rathke's canal. The floor of the respiratory chamber is formed by a layer of transversely disposed fibres, chiefly composed of muscular tissue and coated on the dorsal face by a layer of cells, forming part of the epithelium of the chamber. In the middle line these fibres are more or less interrupted by the raphe described by Stieda; the dorsal aspect of the floor is longitudinally grooved in correspondence with the raphe; and, not unfrequently, the epithelial cells dip down into this groove for a greater or less distance.

On the ventral face of the thick floor of the respiratory chamber

the superficial layer of the integument is naturally separated by a narrow interspace from the transverse fibres of the floor, except in the middle line, where it is attached along a depression or groove corresponding with the raphe, like that of the dorsal aspect of the floor. This layer of integument is thrown into regular and close-set longitudinal plaits, which have been described as muscular fibres by Rathke, Müller, Goodsir, and Quatrefages. Stieda discovered the true nature of these longitudinal fibres; but his figures give no idea of the regularity of the plaits, or of the manner in which the cells of the epidermis line the sides of the folds, which, in transverse sections, have the appearance of glandular cæca. It is this organ which I conceive to be the renal organ, functionally, and to represent the Wolffian ducts, morphologically. These ducts are now known to be formed in the higher Vertebrates by involutions of the lining of that part of the peritoneal cavity which lies external to the generative area. Taking the raphe in *Amphioxus* to represent the line of union of the lateral laminæ, the development of which into the walls of the "perivisceral" cavity has been observed by Kowalewsky, the space between each lateral half of the plaited integument and the ventro-lateral fold of its side, will answer to an involution of the epithelium of the somatopleure, such as that by which the Wolffian duct of osseous fishes[1] commences; and the position of the reproductive gland low down on the wall of the somatopleure is in accordance with this interpretation.

On this view, the wall of the respiratory chamber of *Amphioxus* is strictly comparable to the somatopleure of a higher Vertebrate embryo. On the other hand the cells which line it and represent the peritoneal epithelium must, from the mode of formation of the cavity, occupy the place of the epiblast, and represent a continuation of the epidermis. Thus the respiratory chamber of the *Amphioxus* is an *epicœle*, a cavity of the same fundamental nature as the atrium of the Tunicata; and this circumstance constitutes another curious point of resemblance between the Tunicata and *Amphioxus*.

On the other hand, it is such a cavity as would be formed by the growth and extensive union in the middle line of the lateral prolongations of the wall of the body in *Balanoglossus*.

To what does the respiratory chamber of *Amphioxus* answer in the higher Vertebrata? In the manner of its formation it corresponds, as I have elsewhere[2] suggested, very closely with the respiratory chamber into which the gill-clefts open in the Tad-

[1] Rosenberg, "Untersuchungen über die Entwickelung der Teleostier-Niere," 1867.

[2] Manual of the Anatomy of Vertebrated Animals, p. 121.

pole, and which, in most Anura, communicate with the exterior by only a single external opening on the left side of the body, though there are two symmetrical apertures in the Tadpole of *Dactylethra.* But, in its relations to the alimentary canal, and to the generative and urinary organs, it is obvious that it no less closely answers to the "pleuroperitoneal"[1] chamber of the higher Vertebrates. The opercular fold which constitutes the outer wall of the branchial chamber in the Tadpole is formed by an outgrowth of the body-wall, as Kowalewsky states the wall of the respiratory chamber in *Amphioxus* to be. On the other hand, in all the higher Vertebrata, the somatopleure which bounds the "pleuroperitoneal cavity" seems to be formed by a sort of splitting by the mesoblast, apparently very similar to the process which gives rise to the perivisceral cavity of Annelida and Arthropoda. And the discovery of the free communication of the great serous cavities with the lymphatic system, has removed the objection that might have been urged that the serous cavities of the Vertebrata are not parts of the vascular system.

But it has been seen that it is only by the most careful study of development that the "enterocœlous" "perivisceral cavity" of the Echinoderm has been shown to be morphologically distinct from the "schizocœlous" "perivisceral cavity" of an Annelid; and I think it probable that renewed investigation will prove that the "splitting of the mesoblast" in the Vertebrata represents the invagination of the epiblast in the Ascidian, and the formation of an epicœle by outgrowth of a ridge in *Amphioxus.* Provisionally, at any rate, this hypothesis may be adopted, and the Vertebrata in general, as well as *Amphioxus*, ranked among the Epicœla.

The discovery of the true head, brain, and renal organs of *Amphioxus*, removes the chief supposed anomalies of the structure of this animal, and to so great an extent bridges over the supposed hiatus between it and the Marsipobranchii, with which the development of the latter shows it to be very closely related, that I see no reason for separating it from the class Pisces, in which, however, it may properly rank as the type of a distinct order, which may be termed *Entomocrania*, in contradistinction to the rest, in which, as in all the higher Vertebrates, the skull, even in the embryonic state, exhibits no indication of its primitive segmentation,[2] and which may be termed *Holocrania.*

[1] More accurately "pericardio-pleuroperitoneal" chamber, as the pericardium is only part of it, and, indeed, is only incompletely shut off in the Rays and Myxinoid fishes.

[2] See the proof of this position in my Croonian Lecture, 'Proceedings of the Royal Society,' 1858.

The eye-spots of *Amphioxus* were single in all the specimens I have examined; in the very young *Ammocœtes*, described by Schulze, there are two such pigment-spots, separated by the very short representatives of the cerebral hemispheres and olfactory lobes. This suggests that the eye, like the nose, was primitively simple in the Vertebrata, and that it has become divided in the same way as the nose. In this case the involution of the epiblast, out of which the cornea and the crystalline lens are developed, should have been primitively a median sac; and it is a curious circumstance that, in the very young tadpole, Mr. W. K. Parker, F.R.S., has described and figured a transverse groove connecting the eye-sacs.

I am unable to find anything in the structure or mode of development of the Marsipobranchii which gives this group more than an ordinal value in the class Pisces. Their great peculiarities are the structure of the skull, the presence of a naso-palatine passage which opens posteriorly in the Myxinoids, and the existence of a large superior median brain-lobe.

As respects the first point, the skull is strictly comparable with that of the embryo of any higher Vertebrate, being composed of a parachordal occipital portion, of largely developed trabeculæ, and of auditory capsules. In the Lampreys the cartilaginous hyoidean and mandibular arches are represented, and the curious facial cartilages appear to me to be reducible to the type of the labial cartilages of the Elasmobranchs. The development of the olfactory organ of the Lamprey proves that the single nasal sac of *Amphioxus* is the homologue of the nasal sac of the Marsipobranchii (at least of that part which is lined by the Schneiderian membrane), to which, however, two olfactory nerves, produced apparently by the division of a primitively simple, and median nerve, proceed. The term "Monorhina," applied by Haeckel to the Marsipobranchii, therefore, is not strictly applicable, and I cannot attach any great taxonomic value to the structure of the olfactory organs in this group. The external duplication of the nasal apertures in the higher Vertebrata appears to me to be chiefly due to the fact that, in them, the cerebral hemispheres are thrown out in front of the anterior cerebral vesicle, the front wall of which (the *lamina terminalis* of the third ventricle of the fully developed brain) corresponds with the anterior end of the cerebro-spinal axis of *Amphioxus*, and attains a large size and considerable downward growth before the olfactory sacs are distinguishable. The regions whence the olfactory nerves will be developed are thus widely separated, and thrown to the ventral and lateral aspect of the head, before the Schneiderian membrane is differentiated. It must

also be recollected, that, when the naso-frontal process of the embryo appears, the olfactory sacs become connected with one another by a transverse groove, which is persistent in the Rays, and has the same relations as the middle of the olfactory sac of the Marsipobranchii would have if it were supposed to be transversely elongated.

Recent investigations lead me to think that the lower jaw is by no means wanting in the Marsipobranchii, though it presents a very curious modification. In the Ammocœte the hyoidean cleft, which has been overlooked, is present; and the manner in which the branchial filaments are developed leads me to believe that those which are first formed represent the external gills of the Elasmobranchii, Ganoidei, Dipnoi, and Amphibia.

I have formerly expressed the opinion that the naso-palatine canal of the Marsipobranchii represents the "primitive mouth" of the Vertebrata. The resemblance of the mouth of *Amphioxus* to that of an Ascidian renders this comparison questionable; but, on the other hand, it is a remarkable circumstance that the median nasal involution of *Amphioxus* corresponds very nearly, in its relation to the segmented mesoblast, with the oral aperture of an Arthropod or an Annelid; and it may be that the canal represents the ordinary invertebrate oral passage.

The dorso-median brain-lobe of the Marsipobranch appears to me to be represented in the higher Vertebrata by the peduncle of the pineal gland, which in the embryo is a hollow process of the roof of the anterior cerebral vesicle. It is particularly conspicuous in young Elasmobranchs.

In a few Metazoa, as in some small Rotifera and in the Gordiaceæ. the alimentary canal never becomes developed, although these animals clearly belong to groups in which the alimentary apparatus is normally formed, and may be safely regarded as modified Gastreæ. Whether the like is true of the Cestoidea which are so closely allied with the Trematoda, and of the Acanthocephala, is not certain. Probable as it may be that these are Gastreæ with aborted digestive cavities, it may be well to bear in mind the possibility of their never having passed through the *Gastrula* stage. It is conceivable that an opaliniform *Morula* should, under completely parasitic conditions of life, have developed the organization of a Cestoid worm. At any rate, the contrary must not be assumed without good evidence; and to indicate the doubt, it may be well to establish a provisional group of Agastreæ for these forms.

I subjoin a tabular arrangement of the animal kingdom according to the views expressed in this paper, remarking, in conclusion, that, in my belief, the progress of knowledge will eventually break down all sharp demarcations, and substitute series for divisions.

ANIMALIA.

I. *PROTOZOA.*
- i. MONERA.
  - *Protamœbidæ.* *Protomonadidæ.* *Myxastridæ.* *Foraminifera.*
- ii. ENDOPLASTICA.
  - *Amœbidæ.* *Infusoria flagellata.* *Gregarinidæ.* *Acinetidæ.* *Infusoria ciliata.* *Radiolaria.*

II. *METAZOA.*
- A. GASTREÆ.
  - i. POLYSTOMATA.
    - *Porifera* (or *Spongida*).
  - ii. MONOSTOMATA.
    - 1. Archæostomata.
      - *a.* Scolecimorpha.
        - *Rotifera.* *Turbellaria.* *Trematoda.* *Nematoidea.* *Hirudinea.* *Oligochæta.*
      - *b.* Cœlenterata.
        - *Hydrozoa.* *Actinozoa.* (*Ctenophora*).
    - 2. Deuterostomata.
      - *a.* Schizocœla.
        - *Annelida polychæta.* *Gephyrea* (?). *Arthropoda.*
      - *b.* Enterocœla.
        - *Brachiopoda.* *Polyzoa* (?). *Mollusca.* *Enteropneusta,* *Chætognatha,* *Echinodermata.*
      - *c.* Epicœla.
        - *Tunicata* or *Ascidioida.* *Vertebrata.*
- B. AGASTREÆ (provisionally).
  - *Cestoidea.* *Acanthocephala.*

VI

ON THE RECENT WORK OF THE 'CHALLENGER' EXPEDITION, AND ITS BEARING ON GEOLOGICAL PROBLEMS.

Notices of the Proceedings at the Meetings of the Members of the Royal Institution of Great Britain, with Abstracts of the Discourses delivered at the evening meetings, vol. vii., 1875, *pp.* 354–357. (*Read January 29th,* 1875.)

THE speaker began by commenting on the sailing of H.M.S. 'Challenger' in December, 1872, the nature of her mission, and the completeness and perfection of her equipment, under the auspices of the late First Lord of the Admiralty, Mr. Goschen.

After referring to the course laid down for the 'Challenger,' and her expected return in the spring of 1876, he said that her work is rather more than half done, and that important results had been already obtained, some of which would be especially dealt with in his discourse; but it was necessary, first, to give a sketch of the state of our knowledge on the subject in 1872, in order to do justice to the 'Challenger's' work, without over-estimating its value.

The first successful attempt to ascertain the nature of the bottom of the sea, and of the limit of life at depths greater than five or six hundred feet, was made by Sir John Ross in 1818, who, by the help of a very ingenious machine of his own contrivance, brought up several pounds of mud from 1050 fathoms, or 6300 feet, or about a mile and a quarter, in Baffin's Bay, 72° 30′ N., 77° 15′ W. The nature of what was brought up was described by Ross and by Sabine, who accompanied him. It was a fine greenish mud, but no accurate determination of the nature of this mud was made. Ehrenberg, in 1853, examined the surface scum and the mud obtained by Penny in 73° and 74° N., and found it to consist of

Diatoms (vegetable), which live at the surface.
Radiolaria (animal), which live at the surface.
Sponge spicules (animal), which live at the bottom.

In 1854, Bailey determined the nature of the mud procured by Brooke in 900–2700 fathoms (5400–16,200 feet), in the Sea of Kamschatka. There were absolutely no calcareous organisms in the mud; it was purely silicious. These and other observations in the north circumpolar area tend to establish the existence of a circumpolar zone of silicious deposit in the Arctic regions, within the parallel of 55° N.—a *North Polar silicious cap.*

The speaker next alluded to the despatch of the Antarctic expedition under Sir James Ross, in 1839, and the awakening of attention to the importance of the work done by minute organisms by Ehrenberg, in 1836 and 1838. Ehrenberg discovered that organisms, whose skeletons resemble those which occur in cretaceous and tertiary rocks, and sometimes constitute their whole mass, are still living. The observations of Sir James Ross and Dr. Hooker, at two distant points of the Antarctic zone, proved the existence of a *South Polar silicious cap.*

The speaker then noticed the discovery of the nature of the sediment forming the bottom of the deep sea in the *intermediate zone* (about 110° of latitude), of *calcareo-silicious deposit.* This dates back to 1853, and is due to Ehrenberg's examination of the soundings brought up by Berryman from 2000 fathoms (12,000 feet), between Newfoundland and the Azores. They consisted of silicious *Diatoms*, *Radiolaria*, and *Sponge spicules*, as in the Arctic and Antarctic seas: but the great mass of the deposit was formed of calcareous *Foraminifera.* On these observations Ehrenberg based the conclusion then enunciated, that "chalk is nothing but a heap of dead foraminiferal skeletons."

Professor Huxley then alluded to the confirmation of these results by Bailey, himself, and others, and to the discovery of the extension of a similar deposit over the South Atlantic and into the Indian Ocean; and the further confirmation on a great scale by the 'Challenger.'

Having mentioned Ehrenberg's opinion, that *Globigerinæ*, &c., live at the bottom, and the evidence adduced by Dr. Wallich in confirmation of that view, he referred to Major Owen's results, and to the 'Challenger's' confirmation of the affirmative proposition that they certainly live at the top; he added, that the negative proposition that they do not also live at the bottom is left open. The fact that animals which do live at the bottom feed on the Globigerinæ is probably of no great weight.

The speaker next adverted to the *Greensand deposits* of various geological ages, the nature of which was discovered by Ehrenberg in 1854, and to the nearly contemporaneous discovery of recent greensand (100–300 fathoms) by Pourtales (1854), and the investigation of

its origin by Bailey in 1856; while Parker and Jones subsequently ascertained the formation of greensand to be going on in the Australian seas. The 'Challenger's' discovery of greensand at the bottom of the Agulhas current (200–300 fathoms) was then mentioned. Thus far the value of the work of the 'Challenger' lies in extending and confirming conclusions already more or less established. The next matter is especially her own.

The barrenness of the deeper parts of the Mediterranean, and the existence of a fine clay there, was already known; but no one suspected the existence of extensive deposits of barren clay in the middle of the great calcareo-silicious zone in open ocean.

The dredgings of the 'Challenger' have recently shown that certain deep oceanic valleys contain thick deposits of finely-divided red clay, composed of a silicate of alumina and peroxide of iron. Thus, between Teneriffe and S. Thomas a great valley was found at a depth of about 18,000 feet, the bottom of which was covered with this red material. The origin of such deposits is suggested by the results of some experiments by Mr. Buchanan, the chemist to the 'Challenger,' who, by treating the Globigerina-marl with dilute acids, obtained about 1 or 2 per cent. of insoluble residuum, which strikingly resembled the clay in question. Hence the conclusion drawn by Professor Wyville Thomson, that the great deep-seated deposits of red clay actually represent the remains of marine organisms, of which myriads must have suffered decomposition to furnish these vast accumulations of their *débris*. If this conclusion be correct, not only silicious and calcareous, but argillaceous deposits may be formed by the long-continued action of vital agencies. And as, by well-known processes of metamorphosis, such silicious, calcareous, and argillaceous deposits may be converted into all the chief kinds of rock which constitute the earth's crust, it will follow that rocks of almost any mineralogical composition may be directly or indirectly generated by the action of living organisms. Having discussed various explanations and dismissed them as all at present unsatisfactory, the speaker said that the certainties are:

1. That, beyond certain depths, the calcareous organisms which must fall over the area covered by the ocean disappear, and their place is taken by fine red clay.

2. That when the ordinary Globigerina ooze has its calcareous matter removed, a residuum of fine red clay remains.

But standing firmly on the basis of bare facts, as they are now ascertained, it is permissible to use these facts as a basis for

deductions. Suppose the globe of the earth to be covered with water uniformly to a depth of two thousand fathoms (twelve thousand feet, or about two miles), the merely tidal and current movements which would then exist in the water would be insufficient to cause any important amount of degradation of the solid crust, and there would be no sedimentary deposits worth speaking of.

Now let the lowest forms of vegetable and animal life—*Diatoms*, *Radiolaria*, *Foraminifera*, and *Sponges*—be introduced, and the result would be the formation of the silicious pole caps, and of the calcareo-silicious intermediate zone; and these might accumulate until they formed beds of rottenstone and of chalk, of many thousand feet in thickness.

By well-known metamorphic processes the rottenstone might be converted into a dense opaline rock, or perhaps into quartzite; while the chalk might be converted into crystalline limestone; and in each of these all trace of its origin might disappear.

Next let parts of the bottom in the calcareo-silicious area be raised to within 1000 feet, and others depressed to 18,000 feet. Judging by our present knowledge, the former might be replaced by greensand, and the latter by red clay. The greensand might be metamorphosed into endless varieties of those minerals into which silica, alumina, iron, and potash enter in diverse proportions; the clay into shales, schists, slates, and even into gneiss and granite.

And thus our imaginary world would be covered with more or less extensive patches of all the most important rocks which enter into the composition of the globe, every particle of which would at one time have formed a part of a living organism; though in some, no trace of this primitive composition would remain, and though it is quite possible that all traces of organic life might be obliterated in every one of them.

Application of these results was then made to the reconciliation of an apparent discrepancy between biological theory and geological fact.

1. There is conclusive evidence that the present species of animals and plants have arisen by gradual modification of pre-existing species.

2. There is conclusive evidence that, even geologically speaking, the process has been very slow, and has continued over a much longer period than that which corresponds with the fossiliferous rocks.

3. Nevertheless, beneath the fossiliferous rocks lies a great thickness of unfossiliferous quartzites, sandstones, slates, gneiss, and granite, almost entirely azoic.

These researches consequently lend great support to the views of those geologists who find an explanation of the past history of the rocks in the present operations of nature—views which were held half a century ago by Sir Henry De la Beche, were advocated by Mr. Poulett Scrope, and were still more clearly developed by Sir Charles Lyell, who has so ably elaborated the doctrine of uniformitarianism originally enunciated by Hutton. Sir Charles has, indeed, survived the prejudices which at first opposed his views, and has lived to see most of the reputed heresies of his youth become established as the creed of every philosophical geologist.

VII

ON STAGONOLEPIS ROBERTSONI, AND ON THE EVOLUTION OF THE CROCODILIA.

The Quarterly Journal of the Geological Society of London, vol. xxxi., 1875, *pp.* 423-438. (*Read April 28th*, 1875.)

PLATE XIX. [PLATE 5.]

NEARLY seventeen years ago I had the honour of laying before the Geological Society[1] an account of such remains of a remarkable reptile (*Stagonolepis Robertsoni*) as, up to that time, had been found in the sandstones of the neighbourhood of Elgin, and the conclusion at which I had arrived, "that *Stagonolepis* is, in the main, a Crocodilian reptile."

These remains, however, like all the other fossils from the same district which have come under my notice, were not in a condition very favourable to their interpretation. With the exception of a few dermal scutes, I do not think that a single entire bone, or cast of a bone, has come into my hands; and the most instructive specimens have not been the bones themselves, the osseous matter being always soft, friable, and injured, but their casts in the sandstone. The evidence afforded by the remains of vertebræ and scutes was sufficiently decisive to warrant my conclusion as to the general nature of the animal; but, in respect of the other parts of the skeleton, the surmises which I made in 1858 needed confirmation, or the reverse, by the study of additional materials.

Such materials have from time to time been obtained by the exertions of my friend the Rev. Dr. Gordon, of Birnie, near Elgin, who, aided by a grant from the Donation Fund of the Royal Society, has undertaken the exploration of the fossiliferous beds whenever the

[1] "On the *Stagonolepis Robertsoni* (Agassiz) of the Elgin Sandstones."—Quart. Journ. Geol. Soc. 1859.

operations of the quarrymen laid them bare, and has from time to time sent me consignments of valuable and instructive specimens. From these and others, for which I am indebted to Mr. Grant of Lossiemouth, I have been enabled to make numerous important additions to my knowledge of *Stagonolepis*; so that at present I am acquainted with the following parts of its skeleton:—

1. The dermal scutes, which formed a dorsal and a ventral armour.
2. Vertebræ of the cervical, thoracic, lumbar, sacral, and caudal regions.
3. Ribs.
4. Parts of the skull and teeth.
5. The scapula, the coracoid and the interclavicle.
6. The humerus and (probably) the radius.
7. The ilium, ischium, and pubis.
8. The femur and (probably) the tibia.
9. Two metacarpal or metatarsal bones.

Under these circumstances, it is possible to form a distinct and tolerably complete conception of the nature of *Stagonolepis*, and to compare it with other reptiles, so as to arrive at a just notion of its affinities.

So far as the vertebræ, ribs, scapula, and dermal armour are concerned, I have nothing to alter in the views which I took of the nature of the bones and their systematic significance in 1858. The bone which, in the body of my paper, I interpreted as a coracoid, turns out to have been correctly identified; while that referred to in the note at p. 459, and which led me to doubt whether I was right in this interpretation, has been shown by better specimens to have been an ilium seen from the inner side. The distal moiety of a limb-bone, which is regarded as a femur at p. 452, is shown, by further evidence, to be a humerus; and, finally, the mandible with long curved teeth, which I supposed might belong to *Stagonolepis*, certainly appertains to some other animal.

It is a very remarkable circumstance that, up to the present date, the fossiliferous sandstones of Elgin have yielded remains of *Stagonolepis* (several individuals, some of which must have attained a length of 12 or 14 feet), of *Hyperodapedon* (one almost complete specimen, half another, and fragments of others, the largest probably 6 feet long), of *Telerpeton* (two nearly entire specimens about a foot long), and of the large animal to which the mandible with long curved teeth belonged, and absolutely nothing else. Not a trace of other

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vertebrate or invertebrate animals, or of plants, has yet been detected; and the only other indication of life is the well-known series of footprints, which, so far as I can ascertain, do not occur in the same beds with the reptilian remains. As *Stagonolepis*, at any rate, was a carnivorous animal, and must have needed a considerable supply of aliment, the absence of any trace of the animals on which it fed (unless, as is not very likely, it devoured Lizards) is a curious illustration of the value of negative evidence.

From the evidence which has now been collected, and which consists entirely of specimens associated with the characteristic scutes of *Stagonolepis*, it is demonstrable that, in outward form, this reptile must have resembled one of the Caimans or Jacares of the present fauna of intertropical America, that it possessed strong limbs, of which the anterior were at least as large, in proportion to the posterior, as in the modern *Crocodilia*, but that *Stagonolepis* differed from the Caimans in possessing a long and narrow skull, more like that of a Gavial.

As in the existing Caimans and Jacares, the trunk and tail were protected by a strong armour, composed of a dorsal and a ventral set of thick bony dermal scutes, which, in the trunk, were so arranged as to constitute separate dorsal and ventral shields, while in the tail they formed a continuous girdle. In contradistinction to existing *Crocodilia*, the dorsal shield was made up of not more than two longitudinal series of scutes, and the ventral shield of not more than eight series in any part.

The dorsal scutes are angulated and longitudinally keeled on their free surfaces; the ventral scutes are flat, and formed of a single ossification.

The free surfaces of the scutes have a deeply pitted or grooved sculpture. The vertebræ (except doubtless the atlas and axis) are amphicœlous, the anterior and the posterior surfaces of their centres being alike slightly concave. The transverse processes resemble those of Crocodiles; and as in some recent *Crocodilia* (e.g. *C. niloticus*) and in *Belodon*, those of the anterior thoracic vertebræ are inclined upwards.

The transverse processes of the lumbar vertebræ, of which there were not fewer than two, are long, broad, and directed horizontally, those of the last lumbar vertebra being wider at their outer than their inner ends.

The sacrum consists of two unankylosed, amphicœlous vertebræ; and the ends of the sacral ribs are remarkably wide—more so in proportion than in any Crocodile known to me.

The centrum of the first caudal vertebra is amphicœlous. The skull is produced into a slender rostrum; and the rami of the mandible are united in a long symphysis. The posterior nares are situated far forward, as in Lizards; and neither the palatine nor the pterygoid bones unite to prolong the nasal passage backwards and give rise to secondary posterior nares, as in existing Crocodiles. In the mode of formation of the proper posterior nares, however, *Stagonolepis* conforms to the Crocodilian type.

All the teeth which I have reason to refer to *Stagonolepis* have short, swollen, obtusely pointed crowns, like the back teeth of some existing *Crocodilia*, and they sometimes exhibit signs of wear by mutual attrition.

In the pectoral arch, the scapula resembles that of recent Crocodiles; but the coracoid is short and rounded, like that of the *Ornithoscelida*, and of some existing Lizards, such as *Hatteria*.

As in existing Crocodiles, there is an interclavicle, but no clavicles.

The humerus is more Lacertian than that of existing Crocodiles in the expansion of its ends, and the presence of a ridge and groove on the radial side of its distal end.

The ilium differs from that of existing Crocodiles and is more Lacertian, in the large size of the ala, especially in front, and in the forward prolongation of its anterior dorsal angle; further, in the shape of the ventral margin of the acetabular portion of the bone, and in the absence of any notch or excavation in that margin.

The acetabular end of the ischium resembles that of a Lizard, and not that of a Crocodile; and the rest of the bone is shorter dorso-ventrally, and longer antero-posteriorly, than in recent Crocodiles, in both which respects it closely resembles *Belodon*. The distal end of the femur is narrower in proportion to its proximal end and to the distal end of the humerus than in recent Crocodiles.

Among known forms of Reptilia, the nearest ally of *Stagonolepis* is undoubtedly the *Belodon* of the Upper Keuper of Württemberg, the remains of several species of which have been well figured and described by the late Hermann von Meyer,[1] who makes known the

[1] "Reptilien aus dem Stuben-Sandstein des obern Keupers."—'Palæontographica,' Bände vii., x., xiv. 1861–1865.

Professor Cope ("Synopsis of the Extinct Batrachia and Reptilia of North America"), writing in 1869, and therefore with all the materials for forming a judgment afforded by Von Meyer's publications, takes a very different view of the affinities of *Belodon* from that here adopted.

"*Thecodontia*" (Owen).

"In this suborder we have a singularly generalised group, combining characters of Lizards, Crocodiles, and Sauropterygians. The neural arch of the vertebræ, united by

characters of vertebræ of various regions (though none from the sacrum), very perfect crania and teeth, the scapula, coracoid and humerus, the ilium and the femur. Moreover, during a brief visit to Stuttgart in 1873, Herr Kapff had the goodness to show me a well-preserved pelvis, with the ischium in place.

An extensive comparison can therefore be instituted between *Stagonolepis* and *Belodon* ; and it proves that the two genera closely resembled one another, but, nevertheless, were separated by many differential characters. For example, the teeth are totally different. So far as the nasal apertures are concerned, *Stagonolepis* agrees generally with *Belodon*, though the form both of the external and the posterior nares was different But there can be no doubt that *Stagonolepis* and *Belodon* are members of one and the same natural group, and that this group must be included among the order *Crocodilia*.

The *Crocodilia* are defined from all other Reptilia, whether recent or extinct, by the following characters :—

The transverse processes of the majority of the cervical and thoracic vertebræ are divided into more or less distinct capitular and tubercular portions ; and the proximal ends of the ribs which appertain to these vertebræ are correspondingly divided into capitula and tubercula. The dorsal ends of the subvertebral caudal bones are not united ; the quadrate bone is fixed to the side of the skull ; the pterygoid bones send forward median processes, which separate the palatines, and reach the vomers.

There is an interclavicle, but no clavicles. The ventral edge of the acetabular portion of the ilium is entire, or but slightly excavated. The ischia are not greatly prolonged backwards ; and the pubes are directed forwards and inwards.

The femur has no prominent inner trochanter ; the astragalus is not a depressed concavo-convex bone with an ascending process. There are, at fewest, two longitudinal rows of dermal scutes, one on each side of the middle line of the dorsal region of the body.

suture, and the slightly biconcave centrum, resemble the last two, as also the abdominal ribs. The limbs are rather Crocodilian, the position of the nares Plesiosaurian. The clavicle is Lacertian, while the three vertebræ of the sacrum and the femur are between these and the *Dinosauria*. The most important characters distinguishing these animals from the Sauropterygia are the presence of an elongate sacrum and the more ambulatory form of the limbs. Our knowledge of this order is almost confined to *Belodon* (Meyer), and is derived from that author's descriptions of three large and remarkable reptiles derived from the Keuper of Württemberg—the *Belodon Kapfii* (Meyer), *B. Plieningeri* (Munst.), and *B. planirostris* (Meyer)."

Where did Professor Cope obtain his information respecting the "clavicle" and the sacrum of *Belodon*?

Stagonolepis and *Belodon* come within the order *Crocodilia*, as thus defined, and constitute the first of three suborders, which may be distinguished on purely anatomical grounds.

Suborder I. PARASUCHIA.

Neither the palatine nor the pterygoid bones are produced into osseous plates which prolong the nasal passage and give rise to secondary posterior nares. Consequently the nasal chambers communicate with the mouth by apertures situated beneath the anterior part of the skull. The Eustachian passages are not enclosed by bone. The centra of the vertebræ are amphicœlous. The atlas and axis are unknown. The coracoid is short and rounded. The ala of the ilium is high, and has a large and prominent anterior dorsal angle. The acetabular margin is entire, and its centre projects beyond its anterior and posterior ends. The ischium is short dorso-ventrally, elongated longitudinally, and in its acetabular portion resembles that of a Lizard. The characters of the manus and pes are unknown.

There are two longitudinal series of articulated, carinated, dorsal scutes; and in *Stagonolepis* (but apparently not in *Belodon*) there is a ventral thoraco-abdominal shield, formed of not more than eight longitudinal series of articulated scutes, each of which consists of only one piece of bone.

Genera. *Stagonolepis*, *Belodon*.

Suborder II. MESOSUCHIA.

The palatine bones are produced into osseous plates, which prolong the nasal passages and give rise to secondary posterior nares, which are situated beneath the middle of the skull. The pterygoid bones take no share in the formation of the secondary posterior nares.

A middle Eustachian canal is included between the basioccipital and the basisphenoid, but the lateral Eustachian canals of existing, Crocodilia are represented only by grooves.[1]

The centra of the vertebræ are amphicœlous. The coracoid is elongated, as in the next suborder. The ala of the ilium is less high than in the foregoing, higher than in the following suborder.

[1] M. Eudes Deslongchamps was the discoverer of this and many other important characters of the skull, and, indeed, of the general structure of the Mesosuchia. See the classical "Prodrome des Téléosauriens du Calvados," contained in the 'Notes Paléontologiques,' published by M. Eugène Eudes Deslongchamps in 1869.

Its antero-dorsal angle is at most only slightly prolonged. The acetabular margin is nearly straight, and hardly, if at all, notched.

The ischium is more elongated dorso-ventrally, and is shorter antero-posteriorly, than in the *Parasuchia*. Its acetabular margin is excavated by a deep notch, which marks off a stout pubic process, as in the next suborder.

The manus and pes are constructed as in the next suborder.[1] There are two longitudinal series of dorsal scutes, some of which are longitudinally carinated; and in most, if not all, of the members of this suborder there is a ventral thoraco-abdominal shield composed of not more than eight longitudinal series of undivided flat scutes.

Genera. *Steneosaurus*, *Pelagosaurus*, *Teleosaurus*, *Teleidosaurus*, *Metriorhynchus*, (*Goniopholis ?*, *Pholidosaurus ?*).

Suborder III. EUSUCHIA.

Both the palatine and the pterygoid bones are produced into osseous plates, which prolong the nasal passages backwards, and give rise to secondary posterior nares, situated beneath the hinder part of the skull.

The centra of the vertebræ which succeed the atlas and axis are procœlous, except in the two sacral vertebræ, the opposed faces of which are flat, and the first caudal, the centrum of which is doubly convex.

There is always a middle Eustachian passage enclosed between the basisphenoid and basioccipital, and usually two lateral Eustachian canals likewise enclosed by bone.

The coracoid is elongated.

The ala of the ilium is so low in front as to be almost obsolete; and there is a mere rudiment of an antero-dorsal process. The acetabular margin is deeply notched.

The ischium is elongated dorso-ventrally, and short antero-posteriorly. Its acetabular margin presents a deep excavation, in front of which is a strong process for articulation with the pubis. There are two elongated and constricted proximal carpal bones, and five digits in the manus. In the pes the calcaneum has a strong backward process, and the fifth digit is rudimentary.

There are always more than two longitudinal series of carinated dorsal scutes; and when ventral thoraco-abdominal armour exists, it contains more than eight longitudinal series of scutes.

[1] See d'Alton and Burmeister, 'Der fossile Gavial von Boll," p. 57, and Taf. vii.

The ventral scutes are made up of two ossifications united suturally.[1]

It is obvious, from the mere statement of the characters of these three suborders, that the group which I have termed *Mesosuchia* is intermediate between the other two. It is further plain that the *Parasuchia*, in those respects in which they differ from the *Mesosuchia*, approach the *Ornithoscelida* and *Lacertilia*, especially such *Lacertilia*, with amphicœlous vertebral centra as the existing *Hatteria* and the extinct *Hyperodapedon*, the affinities of which I have elsewhere indicated.[2] In fact I know of no other reptile in which the skull and pectoral arch so nearly approach the structure found in *Belodon* and *Stagonolepis* as they do in *Hatteria*. On the other hand, the *Eusuchia* are those *Crocodilia* which depart most widely from the *Ornithoscelida* and *Lacertilia*, and are the most Crocodilian of Crocodiles.

The differences between the *Mesosuchia* and the *Eusuchia* are of no great moment. The MM. Deslongchamps, in the remarkable memoir to which I have referred, show that in *Metriorhynchus*, which ranges from the Kelloway rock to the Kimmeridge clay, the secondary posterior nares are carried further back than in *Pelagosaurus*, which is confined to the Upper Lias. Let the pterygoids of *Metriorhynchus* begin to unite, and let the posterior faces of the centra of its vertebræ, instead of being a little concave, become a little convex, and it would furnish a perfect transitional form between the *Mesosuchia* and the *Eusuchia*.

On the other hand, the *Parasuchia*, in the conformation of the posterior and the position of the anterior nares; in the non-enclosure of any part of the Eustachian canals by bone; and in the configuration of the coracoid, depart much more widely from the *Mesosuchia*, closely connected with the latter as they are by their dermal armour and in other ways.

From a purely morphological point of view, then, these three suborders of the *Crocodilia* form a series, slightly interrupted between the *Eusuchia* and the *Mesosuchia*, but with a larger gap between the latter and the *Parasuchia*. But whatever the value of the breaks between the three terms of the series, it is clear that the modifications which are needed to connect one term with another are of the

[1] See my papers "On the Dermal Armour of *Crocodilus Hastingsiæ*," Quart. Journ. Geol. Soc. 1859; "On the Dermal Armour of *Jacare* and Caiman, with notes on the specific and generic characters of recent Crocodilia," Proc. Linn. Soc. 1859; and "Etude zoologique sur les Crocodiliens Fossiles Tertiaires," by Dr. Léon Vaillant (Annales des Sciences Geologiques, 1872).

[2] "On *Hyperodapedon*," Quart. Journ. Geol. Soc. 1869, p. 147.

simplest kind, and are throughout of the same order. The kind of change which would convert a Parasuchian Crocodile into a Mesosuchian, would, if continued, convert a Mesosuchian into a Eusuchian. Hence, if there is any valid historical foundation for the doctrine of evolution, the *Eusuchia* ought to have been developed from the *Mesosuchia*, and these from the *Parasuchia*; and if this process of evolution has taken place under such conditions that the skeletons of the *Crocodilia* which have been subject thereto have been preserved, geological evidence should show that the *Parasuchia* have preceded the *Mesosuchia*, and the *Mesosuchia* the *Eusuchia*, in order of time.

Now this is exactly what the geological evidence does prove. It is established that these reptiles appear in the following order:—

PARASUCHIA.

TRIAS. *Belodon, Stagonolepis.*

MESOSUCHIA.

LOWER LIAS.			
UPPER LIAS.			*Steneosaurus, (Mystriosaurus), Pelagosaurus.*
INFERIOR OOLITE.	*		
FULLER'S EARTH.	*		*Teleosaurus, Teleidosaurus.*
GREAT OOLITE.	*		
KELLOWAY ROCK.	*		
		Metriorhynchus.	
OXFORD CLAY.	*	*	
CORAL RAG.	*		
KIMMERIDGE CLAY.	*	*	
PORTLAND OOLITE.			
WEALDEN.			*Goniopholis, Macrorhynchus, Pholidosaurus,* and unnamed Teleosaurians.
LOWER GREENSAND.			
GAULT.			
UPPER GREENSAND.			
LOWER CHALK.			
UPPER CHALK.			*Hyposaurus.*

EUSUCHIA.

Thoracosaurus, Holops, Gavialis (?).

This table shows that the order in which the three divisions of the *Crocodilia* make their appearance is the same as the order of

their departure from the Lacertilian, and approach to the highly specialised Crocodilian, type.

How far back the range of the *Parasuchia* extends we have no means of judging. Nothing is known of them, at present, subsequently to the Upper Trias. Of the two known genera, *Stagonolepis* would seem to approach the *Mesosuchia* somewhat more closely than *Belodon* does, but it is far on the Parasuchian side of the boundary line between the two suborders. There is a hiatus in our knowledge of the *Crocodilia* answering to the Lower Lias, from which, up to this time, no Crocodilian remains are certainly known. With the Upper Lias our acquaintance with the *Mesosuchia* commences; and they are represented, without interruption, as far as the Wealden inclusively. Then follows a great break, answering to the Greensands, Gault, and Lower Chalk, during which period there is no evidence as to the characters of the Crocodilia.

It is at the end of this unrepresented interval that the *Eusuchia* make their appearance, under forms exceedingly similar to the existing long-snouted Crocodiles. Nevertheless the *Mesosuchia* persisted until the end of the Cretaceous epoch. The ranges of the *Eusuchia* and the *Mesosuchia* therefore overlap in the later Cretaceous epoch, where the *Eusuchia* are represented in the Greensands of New Jersey[1] by *Thoracosaurus* (Leidy), *Holops* (Cope), and other forms, and the *Mesosuchia* by *Hyposaurus* (Owen). On this side of the Atlantic the *Gavialis macrorhynchus* of the "Calcaire pisolithique" of Mont Ariné (Upper Cretaceous) and the Maestricht Chalk[2] is a completely differentiated Eusuchian.

It is interesting to observe that *Thoracosaurus* has large præ-lachrymal vacuities like a Teleosaurian, and that the opening of the median Eustachian canal is "a large transversely oval pit" (Leidy, *l. c.* p. 7). The subvertebral processes of the cervical vertebræ are small and divided. Leidy figures a biconvex first caudal vertebra, though it is not certain that it belonged to this genus. I am inclined to suspect that the scute of *Thoracosaurus*, "without any trace of carina" (*l. c.* p. 11), indicates ventral armour.

Hyposaurus had amphicœlous vertebræ; but Leidy states that the anterior concavities of these vertebræ are more deeply depressed than the posterior (*l. c.* p. 20).

On the other hand, *Holops* and *Gavialis macrorhynchus* appear

[1] Leidy, "Cretaceous Reptiles of the United States," Smithsonian Contributions, xiv. 1865. Cope, "Synopsis of Extinct Batrachia and Reptilia," Transactions of the American Philosophical Society, 1869.

[2] Gervais, 'Zoologie et Paléontologie Français,' ed. 1859, pp. 431–457.

to differ very little from existing *Crocodilia*; so that, in the case of the *Crocodilia*, as in that of many other groups, the real "dawn" of the existing fauna is not in the Eocene, but in the latter part of the Cretaceous formation.

Thus the facts relating to the modifications which the Crocodilian type has undergone since its earliest known appearance, are exactly accordant with what is required by the theory of evolution; and the case of the Crocodiles is as cogent evidence of the actual occurrence of evolution as that of the Horses.

It must be understood that in maintaining that the *Crocodilia* were at first *Parasuchia*, then *Mesosuchia*, and lastly *Eusuchia*, I do not suggest that the progression has been effected through the forms with which we happen to be acquainted. At the present day there are two extreme terms of the Crocodilian series, the Gavials being modified in accordance with the needs of an almost exclusively aquatic life, and the Crocodiles and Caimans being much more terrestrial in their habits. It is probable that this distinction has been maintained, and that there have been more aquatic and less aquatic forms throughout the greater part of the existence of the *Crocodilia*.

Unfortunately the only middle Mesozoic *Crocodilia* with which we are well acquainted are the marine, probably sublittoral forms of *Mesosuchia*, such as *Teleosaurus* and *Steneosaurus*; while the older Mesozoic *Crocodilia* are the probably freshwater *Parasuchia*, of a more terrestrial habit.

Thus, before being able to construct the complete ancestral tree of the *Crocodilia*, we need to know those forms (if such existed) of *Parasuchia* which were more aquatic than *Belodon* and *Stagonolepis*—and, on the other hand, those forms of *Mesosuchia* which were less aquatic than the Teleosaurians, and which probably haunted the estuaries and lakes of the Jurassic epoch.

In the present paper I have endeavoured to confine myself to the statement of verifiable facts, and to the conclusions obviously suggested by them; and I abstain, for the present, from dwelling on the bearing of these facts and conclusions on the relation of the *Crocodilia* to other *Reptilia*, especially the *Ornithoscelida*; but I hope to take up that subject on some future occasion.

After the preceding pages were written, it occurred to me that a fragment of a Crocodilian skull from the Wealden of Brook Point, in the Isle of Wight, which has been for many years in the Museum of Practical Geology, might possibly yield some information as to the

condition of the secondary posterior nares in the *Crocodilia* of that epoch. The region in which these apertures should occur was thickly covered with matrix ; but when the latter was removed, very skilfully and carefully, by Mr. Newton, Assistant Naturalist in the Museum of Practical Geology, it revealed the palatine and pterygoid bones, with the base of the skull behind them, in an almost uninjured state (Plate XIX. [Plate 5] fig. 3).

Nothing could be more instructive than the condition of these parts. The nasal passage is narrower, and the posterior palatine foramina are larger, in proportion to the width of the skull, than in any hitherto known Mesosuchian ; the lateral processes of the pterygoids are broader, and the distance between the median Eustachian aperture and the anterior margin of the secondary posterior nostrils far less than in any. The secondary posterior nares themselves are situated relatively further back, and have not a third the dimensions they possess in *Steneosaurus* or *Metriorhynchus* The distance between the posterior margins of the lateral processes of the pterygoids and the occipital face of the skull is greatly less. On the left side, the descending process of the post-frontal, which bounds the orbit behind, is seen. The sculpture upon its outer surface is interrupted close to its ventral end, leaving a smooth narrow groove between the orbit and the temporal fossa, which answers to the much broader groove between the orbit and the temporal fossa in the *Eusuchia*. In all these respects, this Wealden Crocodile approaches the *Eusuchia* much more closely than any previously known Mesosuchian Crocodile does; but it keeps its Mesosuchian character in the manner in which the narrow elongated oval secondary posterior nares are formed. In fact, they are bounded in front by the extreme posterior edge of the palatal plates of the palatine bones, and the pterygoids form only the lateral walls and the septum between the two. The structure therefore lies on the boundary line between that characteristic of the *Mesosuchia* and that which distinguishes the *Eusuchia* ; and as it constitutes a very good generic distinction, the Wealden Crocodile might be made the type of a new genus, if we could compare it with *Goniopholis* and *Macrorhynchus*. Unfortunately there are no well-preserved teeth, and the greater part of the rostrum is absent, while we know nothing of the structure of the secondary posterior nares in either *Goniopholis* or *Macrorhynchus*.

The results obtained from the investigation of the nature and order of the successive changes which the *Crocodilia* have undergone

since their first appearance in the Triassic epoch, naturally suggest the inquiry whether the nearest living and extinct allies of the Crocodiles, the Lacertilia and the Ornithoscelida, which are traceable, the former from the present day to the Permian epoch, the latter from the later Cretaceous to the Triassic epoch, exhibit any evidence of having been subjected to a similar process of evolution.

In the case of the Lacertilia, it is unfortunate that nothing of moment is known respecting the cranial structure of the Permian forms. In the rest of the skeleton it is hard to find any important deviation from the type of the existing Lizards except in the characters of the centra of the vertebræ, which are amphicœlous, instead of being, as in the majority of existing Lizards, procœlous. In the Trias, the only Lacertilia at present known are *Hyperodapedon*, *Rhynchosaurus*, and *Telerpeton* ; and as I have shown on a previous occasion,[1] the first singularly resembles the existing New-Zealand *Hatteria*, the resemblance of which to *Rhynchosaurus* had already been indicated by Professor Owen and Dr. Günther.

In the Museum of Practical Geology, there is a sacral vertebra of a Lizard from the Purbecks, with the anterior face of the centrum concave and the posterior convex. All earlier Lacertilians at present known have amphicœlous vertebral centra, while all but a few existing Lizards are procœlous.

Thus it would appear that, on the whole, the vertebral system of the Lizards has undergone a change corresponding to that which has occurred in the Crocodiles, and that this modification of the articular faces of the vertebræ took place at an earlier period in the Lizards than in the Crocodiles. Apart from this there is no evidence that the Lacertilian type of structure has undergone any important change from the later Palæozoic times to the present day.

The discoveries of American palæontologists prove that the *Ornithoscelida* abounded in the latter part of the Cretaceous epoch, up to the very verge of the commencement of the deposition of the Tertiary rocks.

In a paper on the "Classification of the Dinosauria, with observations on the Dinosauria of the Trias," read before the Society in 1869,[2] I endeavoured to show that there was evidence of the existence of varied forms of Dinosauria in the Trias, and I discussed, at some length, the case of *Zanclodon* (which is probably identical with *Teratosaurus* of von Meyer), from the Upper Keuper of Württemberg.

[1] "On *Hyperodapedon*," Quart. Journ. Geol. Soc. vol. xxv. (1869) p. 138.

[2] Quart. Journ. Geol. Soc. vol. xxvi. (1870) p. 32.

In 1873 I had the opportunity of paying a short visit to Stuttgart; and with the courteous permission and aid of Prof. Fraas, I examined the fine series of remains of *Zanclodon* in the museum of that city. I was thus enabled to assure myself that the rectification of Prof. Plieninger's interpretation of the bone which he terms the ischium, upon which I had ventured (*l. c.* p. 40), was fully justified. It is, in fact, the ankylosed scapula and coracoid. Both the humeri are preserved, and they are about two-thirds the length of the femora. The femora resemble those of *Megalosaurus*. They have a strong inner trochanter; and there is a ridge upon the posterior face of the outer condyle. The tibia has a strong cnemial ridge, though the latter is not so prominent as in *Megalosaurus*. The left tibia and fibula, lacking their proximal ends, are preserved in almost their natural relations. The tibia could not have been more than three or four inches shorter than the femur; and its distal end is very like that of *Megalosaurus*. The fibula is a strong bone, its shaft being about half the diameter of the tibia. About half the astragalus is in place at the distal end of this tibia. It has the characteristic concavo-convex form; but its outer moiety is broken away. A rudiment of the ascending process is traceable; whether it has been broken or not is not clear. The left foot has been dislocated backwards. The proximal ends of three large separate metatarsals lie side by side; and close to them are two distal tarsal ossicles. There appear to have been four (if not five) digits.

It is unquestionable that *Zanclodon* is very nearly allied to *Megalosaurus*; and if, as I think there is little reason to doubt, the fossil named by von Meyer *Teratosaurus*, is the jaw of *Zanclodon*, the affinity is exceedingly close.[1] Inasmuch as the sacrum is composed of a smaller number of vertebræ than in *Megalosaurus*, it may be said that *Zanclodon* is a less differentiated form; but in the absence of a sufficiently complete knowledge of the ventral elements of the pelvis and of the skull, it would be hardly safe to come to any decided conclusion on this point.

At p. 44 of the 'Memoir on the Triassic *Dinosauria*,' to which

[1] I carefully examined the wonderful bone which Plieninger has considered to be a sternum; and Herr Kapff was good enough to show me a fossil representing half a smaller example of the same bone. Plausible as Plieninger's interpretation appears at first sight, I must withdraw my assent to it. The large antero-lateral processes which he figures end, in front, in smooth concave faces, as if they had formed part of a large articular cavity, while at their dorsal and ventral extremities they are rough, as if they had articulated with other bones. The resemblance of these to the pleurosteal processes of the bird's sternum, suggested in my paper, does not hold when they are closely examined. I am much inclined to think that the great shield may represent coalesced ischia.

reference has already been made, I have discussed the characters of the Thecodontosauria, and have shown grounds for arranging them among the Ornithoscelida. On one point I wish to make a correction. Acquaintance with the ilium of *Stagonolepis* convinces me that I have turned the ilium of the Thecodontosauria the wrong way—that what I have termed its anterior end is its posterior end, and *vice versa.* The importance of this fact is that the ilium of *Thecodontosaurus*,[1] thus regarded, instead of being more especially Ornithoscelidan than that of *Megalosaurus*, is in reality much more Lacertilian; and, except for the great vacuity of the inner wall of the acetabulum, it is almost intermediate in form between the ilium of *Stagonolepis* and that of a *Monitor* or *Iguana*.

From the proportion of the ilium to the centra of the vertebræ, it is impossible that more than two vertebræ could have entered into the sacrum, which is again a point of approximation to the *Lacertilia* and *Crocodilia*.

The bone described and figured[2] by Riley and Stutchbury as an ischium is really a humerus, as I have satisfied myself by having the matrix which obscured the distal articular end of the bone cleared away. In the collection of the Bristol Museum there are two of these bones, both belonging to the right side. They are altogether similar in their salient characters to the humeri of a *Monitor*.

Another important point bearing on the affinities of the *Thecodontosauria* is the structure of the distal end of the tibia. I have shown[3] that, in the typical *Dinosauria*, the distal half of the bone is flattened, and has one face turned forwards and outwards and the other backwards and inwards, as in birds. Unfortunately I have been able to find no tibia of *Thecodontosaurus* with the distal end perfect; but, in two specimens, enough is left to show that its distal extremity was not flattened, but was thick with an almost circular transverse section. In fact, in this respect it resembles the tibia of a Lizard rather than that of a Dinosaurian. This structure of the distal end of the tibia necessarily involves the absence of the characteristic Ornithoscelidan astragalus. I may add that, in its form and its approximation to the proximal end of the bone, the inner trochanter of the femur in *Thecodontosaurus* nearly resembles the same part in the *Monitor*, while in the great length of the bones

[1] I use this name without being able to say whether the bones in question belonged really to *Thecodontosaurus* or to *Palæosaurus* (*l. c.* p. 45).

[2] Trans. Geol. Soc. v. pl. 30, fig. 4.

[3] "Further evidence of the affinities between Dinosaurian Reptiles and Birds," Quart. Journ. Geol. Soc. vol. xxv. (1869) pp. 19–22.

of the limbs as compared with the vertebræ there is a further approximation to many Lacertian forms.

The measurements of certain bones found closely associated together enable one to form a tolerably clear notion of the proportions of *Thecodontosaurus*. A right humerus, 6·2 inches long, is associated with the proximal halves of a right femur and a left tibia. Complete specimens of femora and tibiæ of the same size as the foregoing, and lying close together, are respectively rather less than 7 inches and 7·1 inches in length. A fragment of a tibia of approximately the same size is associated with two ilia (right and left) and a centrum of a caudal vertebra. The ala of the ilium measures 4 inches antero-posteriorly. The greatest antero-posterior diameter of the acetabular portion is 2·7 inches. The centrum of the vertebra is 1·2 inch long, 0·6 inch in vertical height.

A strong curved ungual phalanx, 1·15 inches long, lies beside a caudal vertebra of the same length as the foregoing; and a similar phalanx adheres to a metacarpal or metatarsal bone, 3·5 inches long.

Thus it is clear that the *Thecodontosauria* possessed remarkably elongated and, at the same time, strong limbs, differing from those of Lizards only in the somewhat greater size and lower position of the inner trochanter of the femur, and in the large cnemial end of the tibia, but devoid of the special peculiarities observed in the ankle-joint of the typical Ornithoscelida. We unfortunately know nothing of the structure of the ventral elements of the pelvis. The ilium, as has been seen, is Lacertilian in form, Ornithoscelidan in the character of the acetabulum. But the vertebræ and the implantation of the teeth are, as in the typical Ornithoscelida, Crocodilian, and not Lacertilian.

Such evidence as the imperfect materials at present extant offer tends to show that the Triassic Thecodontosauria were devoid of some of the most marked peculiarities of the later Ornithoscelida; while, on the other hand, the most ornithic of Ornithoscelida at present known, such as *Iguanodon*, *Hadrosaurus*, *Hypsilophodon*, and *Lælaps*, belong to the later half of the Mesozoic period.

Just as the oldest Crocodiles differ less from the Lacertilia than the recent Crocodiles do, so it appears that the oldest Ornithoscelida approached a less differentiated Lacertilian form. The Crocodilia and the Ornithoscelida appear to converge towards the common form of a Lizard with Crocodilian vertebræ.

On the evidence of such remains of *Cetiosaurus* as had come to light in 1869 I have assigned a place among the Dinosauria to that reptile. The materials subsequently brought together and described

by the late Prof. Phillips do not, however, bear out this view, but show that *Cetiosaurus* is, like a Thecodontosaurian, a reptile with a vertebral system similar to that of the Ornithoscelida and Crocodilia, but with more Lacertilian limbs ; and it may be that *Stenopelyx* is in the same predicament. If further information confirms this suspicion, it will probably be convenient to separate the *Thecodontosauria*, *Cetiosaurus*, and perhaps *Stenopelyx*, as a group of the Suchospondylia, distinct from the Ornithoscelida on the one hand, and the Crocodilia on the other, under the name of "Sauroscelida."

EXPLANATION OF PLATE XIX. [PLATE 5.]

View of the palatine face of the posterior half of the skull in one Eusuchian and three Mesosuchian Crocodiles, showing the modifications in the form and position of the secondary posterior nares.

Fig. 1. *Steneosaurus Larteti.* (Deslongchamps, "Notes Paléontologiques," pl. xiv. fig. 2.)

2. *Metriorhynchus Blainvillii.* (Deslongchamps, ibid. pl. xx. fig. 1 *b.*)

3. The Crocodilian skull from the Wealden at Brook Point, in the Isle of Wight. Of the natural size.

4. *Gavialis gangeticus.* (D'Alton and Burmeister, 'Der fossile Gavial von Boll,' pl. iv. fig. 2.)

DISCUSSION.

Prof. DUNCAN said that it was impossible to criticise a paper of this kind, and that it would perhaps be a greater compliment to give a silent assent to the author's statements. At the same time he remarked that in teaching Indian geology he had been much struck by the homotaxis of the strata above the Indian Coal-bearing beds and those containing *Stagonolepis* in Scotland. In the Trias of India a Parasuchoid Crocodile was associated with *Hyperodapedon*, and a Dicynodont gave an African facies to the fauna. He thought the history of the evolution of the Crocodilia would have to be worked out in India, but remarked that none were known there between the Trias and the Sewalik deposits. He inquired of Prof. Huxley whether there was any alliance between *Stagonolepis* and *Parasuchus*, and what had been made out with respect to the structure and analogies of the latter genus. He considered that the case established by Prof. Huxley with regard to the Crocodiles furnished a stronger support to the hypothesis of evolution than even that of *Hipparion* and the Horse.

Mr. EVANS remarked that the paper was a most interesting and important contribution to the literature of evolution. Referring to the differences in the position of the nostrils, he suggested that it would be a great gain if these could be correlated with differences in the mode of life, as thus we should probably acquire some clue to the causes of the successive modifications of the type.

Prof. SEELEY saw no ground for doubting the value of Prof. Huxley's conclusions with regard to *Stagonolepis*, but thought it might be for the advantage of science to have other ways of looking at the evolution of the Crocodilia. He was not inclined to believe that the characters of the base of the skull, which Prof. Huxley had dwelt upon, afforded ground for a subdivision of the Crocodilian type -not only because he thought the character insufficient in itself among Reptiles, but because he did not believe that the characters of the older group were in any way Lacertilian. He spoke of the great range both of osteological

Fig. 3.

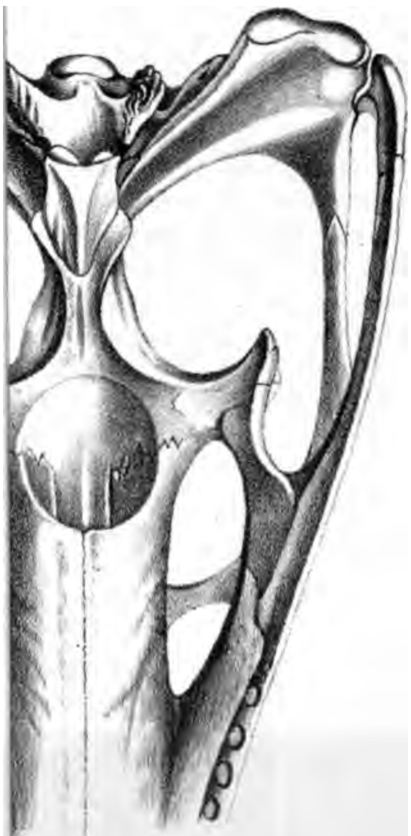


Fig. 1.

T. Way, imp.

character and vital organization in the existing Lacertilia, which rendered it difficult to know exactly to what the author specially referred; and he pointed out that the Lacertilians were surviving types from which *Stagonolepis* could not be supposed to have descended, unless the Lacertilian type had remained unchanged, and the Crocodilian type had alone been developed. Hence, seeing the numerous Lacertilian characters in the limbs of Chelonians, he inquired of the author whether he would not be disposed to consider the few Lacertilian features of *Stagonolepis* as due to the conditions of existence rather than as resulting from descent.

Prof. HUXLEY, in reply, stated that the Indian Crocodile (*Parasuchus*) was very like *Belodon* in the jaw and teeth, the scapular and coracoid, the vertebræ, the ilium and the tibia. The tibia had the proximal end like that of a Lizard, the distal like that of a Crocodile. Additional remains from India furnish a new point of resemblance between the Indian deposits and those of Elgin. With regard to the difference in the position of the nostrils, he did not know that any reason could be given for this, unless the modification might facilitate respiration when the animal was engaged, after the manner of Crocodiles, in drowning its prey; but this would not hold good in the case of the Gavial, which feeds on fish. The food of *Stagonolepis* was doubtful: the teeth were often more or less ground down. In reply to Prof. Seeley, he stated that his comparisons were not founded on the skull alone, but on the other principal characters. As to the older Lacertilia, he had paid some attention to them, and considered that in all their essential characters they resembled the existing forms: the modern *Sphenodon* (or *Hatteria*) of New Zealand was singularly like the Triassic *Hyperodapedon*. The skull of *Belodon* has many curious resemblances to that of *Hatteria*. His conclusion was, that the existing Lacertilia were little modified, and the existing Crocodilia much modified, descendants from a common ancestral from of palæozoic age.

VIII

CONTRIBUTIONS TO MORPHOLOGY. ICHTHYOPSIDA. —No. I. ON *CERATODUS FORSTERI*, WITH OBSERVATIONS ON THE CLASSIFICATION OF FISHES.

Proceedings of the Scientific Meetings of the Zoological Society of London for the year 1876, *pp.* 24–59. (*Received January 4th*, 1876.)

TWO specimens of *Ceratodus forsteri* have come into my possession within the last two years. The first was kindly placed at my disposal by the Secretary of this Society some time ago; but I was unwilling to dissect it until I had a second. This desideratum was supplied by my friend Sir George MacLeay, who, on a recent visit to Australia, was kind enough to undertake to obtain a *Ceratodus* for me, and fulfilled his promise by sending me a very fine and well-preserved fish, rather larger than the first. The first was 32 inches long, the second only 30 inches, though a considerably stouter fish.

I need hardly say that I have little to add or qualify in the general description of the exterior structure given by so accomplished and experienced an ichthyologist as Dr. Günther.[1] Only in one point do I find my interpretation of the facts widely discrepant from his; and that is in regard to the position of the external nostrils.

Dr. Günther says, "As in *Lepidosiren*, there are two nasal apertures on each side, both being situated within the cavity of the mouth."

That anterior nasal apertures should be situated, in any sense, "within the cavity of the mouth," would be so singular a deviation from the otherwise universal rule, that the anterior nares of vertebrated animals are situated outside the mouth, on the surface of the head, that conclusive evidence must be producible before the anomaly can be admitted to exist; and, so far as my observations go, that conclusive evidence is not only wanting, but the contrary is demonstrable.

[1] 'Description of *Ceratodus*,' Phil. Trans., pt. ii. 1871.

In *Ceratodus*, it is easily seen that the anterior nares are not occluded when the mouth is shut by the apposition of the edges of the mandible to the palate. The anterior nares, in fact, lie altogether outside and in front of the contour of the mandibles, on the under concave surface of the anterior part of the head. The median portion of the margin of this region of the head must not be confounded with the upper lip, with which it has nothing to do. The maxillary portion of the upper lip is, in fact, represented only by a fold of the integument, which begins on the outer side of the anterior nostril, and extends back to the angle of the gape, where it passes into the lower lip. The præmaxillary, or internasal, portion of the upper lip is represented by a delicate fold of the integument, disposed in a transverse arch in front of the vomerine teeth, which it separates from the inner boundary of the anterior nares. The outer and posterior portion of the lower lip is produced into a free process, which is folded back against the jaw, and extends for about two thirds of the distance from the angle of the mouth to the symphysis, ending by a rounded free edge.

Thus the anterior nares can in no sense be said to open into the cavity of the mouth, inasmuch as they lie outside the præmaxillary portion of the upper lip, and are not enclosed by the maxillary portion of that lip. They are not even placed between the upper and the lower lips, inasmuch as the vaulted flap, on the underside of which they lie, is not the upper lip, but the anterior part of the head.

In *Lepidosiren*, the anterior nares are closer to the anterior margin of the head than in *Ceratodus*, and the præmaxillary lip is represented only by a papillose ridge, in which the integument of the underside of the head, between the anterior nares, terminates posteriorly. Otherwise the disposition of the nostrils is quite as in *Ceratodus*; and when the mouth is shut, the nostrils open on the underside of the head, in front of it and of the rudimentary præmaxillary portion of the upper lip.

The disposition of the nasal apertures in the Dipnoi is essentially Selachian.[1] In the common Dogfish (*Scyllium*), for example, the anterior contour of the head answers to the anterior contour of the head of *Ceratodus*. The mandibular and maxillary lips are similarly disposed; and the external nares are placed on the sides of the head in a similar position. But the præmaxillary part of the upper lip is much larger and more prominent; and its outer edges (septal alæ), instead of being continued into the maxillary lip, to form the floor of

[1] See the excellent observations of Gegenbaur, 'Kopfskelet der Selachier,' p. 224 *et seq.*

the nasal passage, are separated from it by a fissure, which communicates with the nasal cavity. This fissure is overlapped by the septal alæ ; and thus an incomplete nasal passage, which opens posteriorly into the cavity of the mouth, is constituted.

Still more instructive is the comparison of the nasal passages of *Ceratodus* with those of *Cestracion* and *Chimæra*. In *Cestracion*, the external nostrils lie just outside the mouth, the lower lip coming into contact with the maxillary and præmaxillary portions of the upper when the mouth is shut. The anterior end of the maxillary lip is folded in, and passes into the external part of the *ala nasi*, which has a thickened edge, and ends in a continuation of the free fold of the lip. The inner *ala nasi* is the outer part of the internasal or præmaxillary part of the upper lip. It also ends in a free edge, which is rolled inwards. The septal ala and the maxillary ala do not unite ; but a groove is left between their convex edges, which answers to part of the groove which leads from the nose into the mouth in Dogfish and other Plagiostomes. But the greater part of this groove is represented by a canal formed by the convoluted septal ala which is open on its dorsal aspect, and communicates, in front, with the cavity of the olfactory sac. Behind, the free edge of the septal ala has a curious fringe ; and when the mouth is shut, this fringe overlaps the edge of the mandible. The free edge of the septal ala bounds a large opening, the posterior nostril, which is situated, as in *Ceratodus*, at the point of junction between the vomerine and the palatine teeth. Consequently, when the mouth is shut, there is a free passage for water through this incompletely closed nasal canal.

An arrangement of a very similar character exists in *Chimæra*. Here the nasal septum is very narrow, but widens out below, where, as the præmaxillary lip, it overlaps the vomerine teeth. The free edge of the septal ala is curved in, as in *Cestracion*. Meeting it is an inward process of the maxillary lip, which abuts against the septal ala in the same way as the maxillary ala does in *Cestracion*. Outside this, again, is another flap-like process of the maxillary lip, which overhangs the foregoing when the maxillary lip is in place. Between the præmaxillary lip and the maxillary lip is the nasal passage, open ventrally as in *Cestracion* ; and an interval between the vomerine and palatine teeth above and the mandibular tooth below (the posterior nostril) places this passage in free communication with the oral cavity.

It is obvious that if the septal and the maxillary alæ in *Scyllium*, *Cestracion* and *Chimæra* united along the middle line, such a nasal passage as exists in *Ceratodus* would be the result. Compared with

Ceratodus, the Elasmobranchs mentioned are hare-lipped; and as regards the position of the external nostrils, *Cestracion* and *Scyllium* are intermediate between *Chimæra* and *Ceratodus*.

It may be asked, what is the use of a nasal passage and of internal nares in a purely branchiate animal? Without actual experiment it is hard to give a definite answer to this question; but I will venture upon two suggestions. In the first place, these communications between the cavity of the mouth and the exterior must permit slow respiration to take place when the jaws are shut; and it is easy to imagine that this, under many circumstances, may be an advantage.

In the second place, the large olfactory sacs of these animals suggest that the sense of smell is of value to them; and the communication of the nasal passages with the mouth must enable them to do what they could not do otherwise—namely, accelerate the rapidity of the contact of odoriferous particles with the Schneiderian membrane at will. The fish with posterior nasal apertures, in fact, can "sniff" effectually, while that operation could only be very imperfectly performed by compression and dilatation of the walls of the olfactory sacs in the absence of any second opening. Probably the second opening so generally present in the olfactory sacs of the Teleostei, and the naso-palatine canal of the Marsipobranchs, have a similar physiological significance. In *Ceratodus* there is the further physiological relation to aerial respiration; and in all the higher Vertebrata the nasal passages are concerned in sniffing and breathing.

With respect to the internal structure of *Ceratodus*, I shall confine my remarks, in the present communication, to the brain, the skull, and the pectoral limbs. *Ceratodus* is, in fact, the most surprisingly suggestive animal I have ever had occasion to study; and the attempt to comprehend the morphological significance of the organs I have mentioned has led me so far, that I must defer the consideration of other parts of its organization to another occasion.

I. *The Brain.*

I had no great hope of finding the brain in a state fit for examination in my specimen of *Ceratodus*; and in fact the cerebral substance and that of the nerves are in a very friable condition. But, by great good fortune, the *pia mater* is so very dense and tough, that it has held the cerebral substance in place; and thus not only the external form, but somewhat of the internal structure of the brain could be satisfactorily determined.

The brain is represented from above in fig. 1, from the left side in fig. 2, and from below in fig. 3.

The brain of *Ceratodus* nearly fills the cranial cavity, the interspace left between it and the walls of the latter being, to a great extent, occupied by a peculiar reticulated tissue. The *medulla oblongata* is long and slender, but widens, anteriorly, in the region of the fourth ventricle. This cavity is arched over by a *tela vasculosa* (*Tv*, figs. 1 and 2), separated into two lateral convexities by a slight

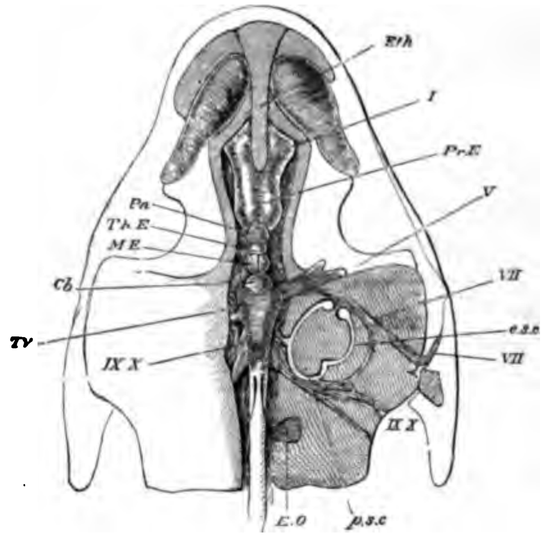


FIG. 1.—*Ceratodus forsteri.* Dorsal view of the brain *in situ*.
Pr E, *lobus communis* of the prosencephalon ; *Th.E*, Thalamencephalon ; *Pn*, pineal gland ; *ME*, mesencephalon (the median groove is somewhat too strongly marked) ; *Cb*, cerebellum ; *Tv*, tela vasculosa over the fourth ventricle ; *e.s.c*, *p.s.c*, external and posterior semicircular canals ; I, V, VII. IX, X, cerebral nerves ; *E.O*, exoccipital ossification. The general contour of the chondrocranium is given ; on the right side the cartilage has been sufficiently removed to show the anastomosis of the seventh and ninth nerves, the auditory organ, and other deep-seated parts. With respect to this and the other figures, I may remark that my object has been to make accurate diagrams drawn to scale, and not pictures.

median depression. In front, each convexity is continued into a blind rounded cornu, which lies over the origin of the fifth and seventh auditory nerves. The two cornua diverge, and the cerebellum is continued backwards as a triangular lamella between them. The cerebellum is relatively very small, being represented merely by the thin arched roof of the anterior part of the fourth ventricle. In front of it is a rounded elevation, obscurely divided by a longitudinal depression into two. These are the only indications of the optic lobes of the mid brain, or mesencephalon. In front of this is the

fore brain. The hinder division (or thalamencephalon) is narrower than the mesencephalon, and passes below into the infundibulum, which terminates in the large, oval, flattened, pituitary body (*hypophysis*). This is lodged in an excavation of the cartilaginous floor of the skull representing the *sella turcica*.

Dorsally, the thalamencephalon is continued upwards and forwards into the subcylindrical peduncle of the pineal gland (*epiphysis* or *conarium*). This is a large heart-shaped body, the base of which is turned downwards and backwards. The apex is connected by

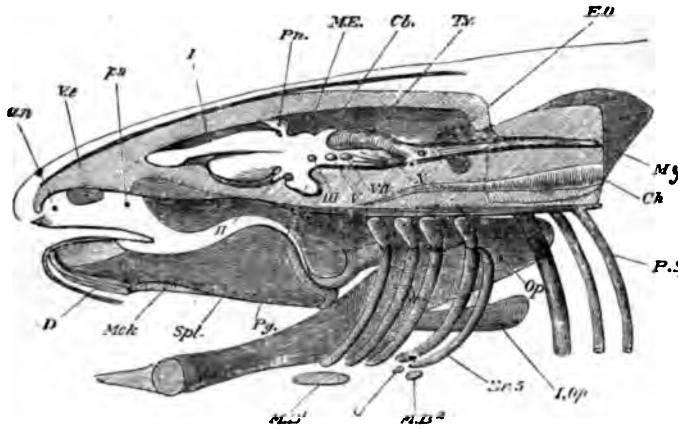


FIG. 2.—*Ceratodus forsteri*. Left lateral view of the brain *in situ*.
The details of the structure of the dorsal region of the spinal column are omitted. *Ch*, notochord; *E.O*, exoccipital ossification; *P.Sph*, parasphenoid; *Vt*, vomerine teeth; *an*, *pn*, positions of the anterior and posterior nares; *Op*, operculum; *I.Op*, interoperculum; *Spl*, splenial, and *D*, dentary bones of the mandible; *Mck*, Meckel's cartilage; $M.B^1$, $M.B^2$, anterior and posterior mesobranchials; *Br.* 5, fifth branchial arch; 6, nodule of cartilage, which possibly represents a rudimentary sixth arch; *Py*, pituitary body. The other letters have the same signification as in the preceding figure. The suprascapular bone is shown in place; and its contour is given as if the anterior part of the vertebral column were transparent.

fibrous and vascular tissue with a depression in the cartilaginous roof of the skull.

Next follows the largest division of the brain, answering to the cerebral hemispheres and the olfactory lobes. The former are represented by a single oval *lobus communis*, the middle area of the roof of which is occupied by a broad thick *tela vasculosa*. From the anterior dorsal aspect of the prosencephalon proceeds, on each side, the large olfactory lobe, which, flattening in front, and becoming obliquely truncated, terminates against the posterior walls of the olfactory sacs. A backward prolongation of the mesethmoid cartilage separates the two lobes. In the lateral view of the brain (fig. 2) the

manner in which the olfactory lobes take their origin from the dorsal aspect of the prosencephalon is well seen. The short and thick infundibulum, terminating in the flattened oval pituitary body, and the origins of the second, third, fifth, eighth, ninth, and tenth nerves are shown.

The ventral view (fig. 3) displays the origins of the small optic nerves (II) which arise close together from the floor of the thalamencephalon. Whether any *chiasma* exists could not be ascertained.

FIG. 3.—*Ceratodus forsteri.* Underview of the brain (nat. size).

I, olfactory, II, optic, VI, third nerve (?); V, VII, IX, X, roots of the trigeminal, portio dura, auditory, glossopharyngeal, and pneumogastric nerves; *v.c*, one of the lateral ventricles of the *lobus communis*, laid open from below.

In the middle line of its ventral aspect the prosencephalon presents a deep longitudinal fissure, lodging anterior cerebral arteries. The walls of the fissure have been separated by turning the left division of the prosencephalon to one side; and the floor of the ventricle (*v.c*), which is contained in the prosencephalon, has been removed.

When the dorsal wall of the brain was cautiously laid open by a median section, it was found to contain one large ventricular cavity the separation of which into fourth and third ventricles was indicated only by slight constrictions of the roof and side walls. The large ventricle of the prosencephalon is partially separated into two chambers by a median septum, formed by the infolding of its ventral wall; and the spacious ventricle of each olfactory lobe opens into the dorso-lateral part of each of these chambers.

The place and mode of origin of the olfactory and of the optic nerves have already been mentioned.

The third nerve is indicated in the figure; but I am somewhat doubtful as to the nature of the cord thus marked.

No fourth or sixth nerve was observed.

The fifth arises by a single large cylindrical root just below the anterior end of the cornu of the tela vasculosa of the fourth ventricle. The seventh and eighth leave the medulla by a common root just behind this; and the roots of the ninth and tenth nerves, divided into three bundles, arise from a tract at the sides of the medulla which extends from the last to the hinder limit of the *tela vasculosa*, and incline obliquely backwards to their exit.

The brain of *Ceratodus* is very singular and interesting, inasmuch as it presents resemblances to that of the Marsipobranchii on one side, to that of the Ganoids and Amphibia on another, and to that of the Chimæroids and Plagiostomi on a third.

As in the brain of the Marsipobranchii, the pineal gland is relatively very large, with its pointed dorsal end inclined upwards and forwards, and the roof of the fourth ventricle is almost entirely formed by the *tela vasculosa* ; but, as in the Ganoidei and Amphibia, the cerebellum is larger than in the Lampreys. In *Ceratodus* it is similar to, though proportionally less than that of *Lepidosteus*, and still more like that of *Polypterus*. In the proportions of the thalamencephalon the brain of *Ceratodus* resembles that of the Sturgeon and that of the Ray ; while in the representation of the cerebral hemispheres, or prosencephalon, by a large imperfectly divided *lobus communis*, from the dorso-lateral regions of which the olfactory lobes take their rise, the brain of *Ceratodus* presents a feature hitherto known, so far as I am aware, only in the Plagiostomi.[1] Thus, in its cerebral characters, *Ceratodus* occupies a central place in the class Pisces.

The development of the cerebral hemispheres in Plagiostome fishes differs from the process by which they arise in the higher Vertebrata. In a very early stage, when the first and second visceral clefts of the embryo of *Scyllium* are provided with only a few short branchial filaments, the anterior cerebral vesicle is already distinctly divided into the thalamencephalon (from which the large infundibulum proceeds below, and the small tubular peduncle of the pineal gland above, while the optic nerves leave its sides) and a large single oval "vesicle of the hemispheres." On the ventral face of the integument covering these are two oval depressions, the rudimentary olfactory sacs.

As development proceeds, the vesicle of the hemispheres becomes divided by the ingrowth of a median longitudinal septum, and the olfactory lobes grow out from the posterior lateral regions of each "ventricle" thus formed, and eventually rise on to the dorsal faces of the hemispheres, instead of, as in most Vertebrata, remaining on their ventral sides. I may remark that I cannot accept the views of

[1] So far as I can judge from the examination of a small but well-preserved specimen of *Lepidosiren annectens*, for which I am indebted to Mr. Sclater, the brain of this fish is similar, in all essential respects, to that of *Ceratodus*. The figure of the brain of *Lepidosiren* given by Prof. Owen in his 'Anatomy of Vertebrates' is susceptible of interpretation in this sense. Hyrtl's description and figure of the brain of *Lepidosiren paradoxa* ('Abhandlungen der königlichen böhmischen Gesellschaft,' Bd. iii. 1845), on the other hand, leave me in doubt whether, apart from its curious asymmetry, the brain of this fish does or does not present important differences from that of *Ceratodus* and that of *Lepidosiren annectens*.

Miklucho-Maclay, whose proposal to alter the nomenclature of the parts of the Elasmobranch's brain appears to me to be based upon a misinterpretation of the facts of development.

II. *The Skull.*

Dr. Günther[1] distinguishes in the skull an "inner cartilaginous capsule and an outer incomplete osseous case, to which again some outer cartilaginous elements are appended. In the former the confluence of cartilage is so complete, that no distinct divisions are traceable by sutures; its parts can be designated only by reference to the locally corresponding bones of the teleosteous skull."

This would seem to imply that the chondrocranium of vertebrated animals is formed by the coalescence of parts analogous to those which compose the bony skull of osseous fishes. As a matter of fact, however, the chondrocranium is never formed of such elements, but is built up, at a very early stage of embryonic development, by the union of primitively distinct parachordal, otic, and pleural elements,[2] which in no way correspond with the bones of the teleostean skull. And when Dr. Günther subsequently (*l. c.* p. 522) speaks of "three groups of superficial labial cartilages," the "upper labial," the "supraorbital," and the "lower labial," the discrimination of such cartilages must, I think, be regarded merely as regional anatomy; and it must not be supposed that they have anything to do with the cartilages to which the same names are applied in other fishes, several of which exist in *Ceratodus*, and will presently be described.

When the osseous and merely fibrous structures are carefully removed, I find that the chondrocranium (figs. 4, 2, and 7) consists of a continuous cartilaginous mass, the interorbital region of which is much narrower than any other part, produced inferiorly and laterally into two stout suspensorial or palato-quadrate processes, with the pulley-shaped ventral ends of which the strong Meckelian cartilages are articulated. Anteriorly the orbits are bounded by the *antorbital processes* (*A.O*), which curve downwards in front of the eye. From these antorbital processes the cartilage is continued forwards to form the evenly curved roof of the ethmoidal region and its contained nasal chambers, and, bending down on all sides, ends in a free edge, which is slightly concave opposite each anterior nasal opening (*an*, fig. 4), and much more deeply excavated opposite the posterior nares (*pn*, fig. 4). The small process (*a*) which lies between the two

[1] *L. c.* p. 521.

[2] 'On the Structure of the Skull, &c., of *Menobranchus lateralis*,' P. Z. S. 1874.

excavations in question is connected by a strong fibrous band with the antorbital process (*A.O*), and this, by the ossified bar described by Dr. Günther, with the *postorbital process* (*P.O*); but these structures have nothlng to do with the chondrocranium. Behind the orbits, the skull suddenly widens out into two broad periotic masses, which lodge the auditory labyrinth. Anteriorly and ventrally these processes are continued into the suspensorial pillars (*Qu*); while behind they pass into thin but wide cartilaginous plates (*O, C*, fig. 4), which roof over the chambers in which the branchiæ are lodged.

I thought at first that *Ceratodus* had no labial cartilages; but at length I discovered two small upper labial cartilages in their right places, namely in the region of the nostrils.

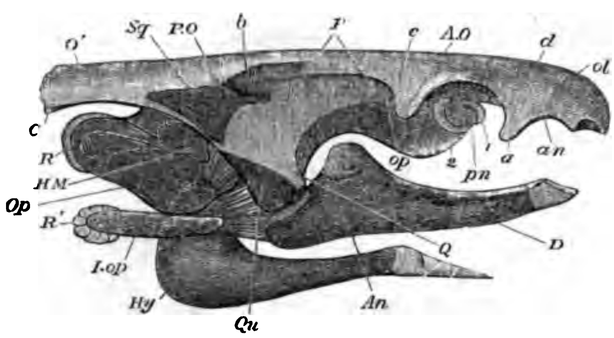


FIG. 4.—*Ceratodus forsteri.* Lateral view of the chondrocranium, with most of the bones and fibrous tissues removed.

ol, position of the olfactory sac; *an*, *pn*, position of the anterior and posterior nares; *a*, process of the cranial cartilage, *d*, between the two; 1, 2, upper labial cartilages; *op*. optic foramen; *A.O*, antorbital process; *P.O*, postorbital process; *P.Q*, palato-quadrate process; *Sq*, *Qu*, remains of the bony plate which lies on the outer side of this process; *O.C*, occipital prolongation of the chondrocranium roofing over the branchial cavity; *D*, dentary; *An*, angular; *Hy*, hyoid; *I.op*, interoperculum; *Op*, operculum; *R*, *R'*, cartilages representing hyoidean rays; *HM*, hyo-mandibular.

One of them (1, figs. 4 and 5) lies in the roof of the mouth, just in front, and on the inner side of, the posterior nasal aperture. It is fixed to the mesethmoidal cartilage (*M.E*) by fibrous bands, and is broader behind than in front. The inner edge of this cartilage is concave, the outer convex, and it has a nearly horizontal direction.

The second cartilage (2, figs. 4, 5, 7) is stouter, and lies behind and on the outer side of, the posterior nasal aperture. Its dorsal end is attached to the base of the skull and anterior part of the palato-quadrate cartilage just above the middle of the palatine tooth. It thence descends with an outward convexity and inward concavity, and terminates in the upper lip near the angle of the mouth.

Dr. Günther states (*l. c.* p. 524) that "the body of the mandible

is persistent cartilage; but its entire outer and inner surfaces are covered by bone, forming an articular and a dentary piece. . . . . . The articular and dentary bones meet near the top of a low but strong coronoid process, and again at the symphysis, which is formed by fibrous tissue, and may easily be separated by the knife . . . . In front of the jaw the cartilage is expanded into a slightly concave lamella (lower labial cartilage)."

I find a persistent Meckelian cartilage, such as that here described; but as, after careful removal of the ensheathing bones, I have been unable to discover any separation between this lamellar expansion and the rest of the cartilage, I am in doubt whether the lamella represents the lower labial cartilage or not. The analogy of the

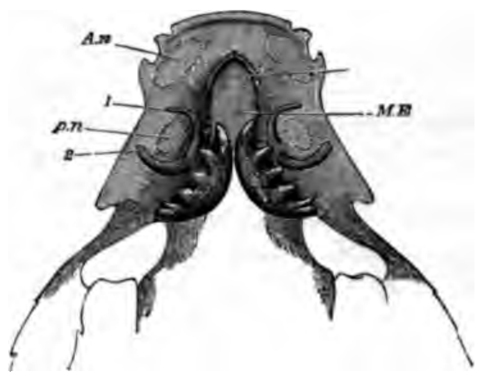


FIG. 5.—*Ceratodus forsteri.* Underview of the skull, showing the vomerine teeth (*V.t*), the palatine teeth, the mesethmoid cartilage (*ME*), and the upper labial cartilages (1, 2) in place. The dotted lines *An*, *p.n* indicate the form and position of the anterior and the posterior nares.

Frog, however, leads one to suspect that distinct lower labial cartilages may exist in the young *Ceratodus.*

Dr. Günther does not mention a third ensheathing bone (figs. 2 and 4, *D*) which is united by a suture with the other two, and lies on each side of the symphysis on the ventral face of the mandible. It is a flat plate, of a triangular form, with a thick rugose inner edge for the attachment of the symphysial ligament. Its posterior edge is thin and concave; its external edge is also thin and overlaps the bone termed "articular" by Dr. Günther, uniting with it by a squamous suture. The outer half of its dorsal aspect is smooth, and helps to support the ventral face of Meckel's cartilage; the inner or symphysial half presents a broad, rough triangular surface, which extends on the inner side of the symphysial end of Meckel's cartilage, and unites with a

corresponding surface furnished by the expanded symphysial end of the bone, termed "dentary" by Dr. Günther. I cannot doubt that this bone is the representative of the true "dentary" element; nor is there any question in my mind that Dr. Günther's "dentary" is the true "splenial" element, while his articular answers to the "angular" piece of the vertebrate mandible. In the attachment of the tooth to the splenial, and not to the dentary, element, *Ceratodus* presents an interesting and important feature of resemblance to *Siren* and to larval Salamanders on the one hand, and, on the other, to *Polypterus.*

The splenial element in this Ganoid resembles that of *Ceratodus*, not only in bearing teeth, but in form, position, and relative size. In a young specimen of *Polypterus* I find that the splenial does not extend continuously to the symphysis, but that, between its anterior termination and the latter, there are two short and broad bony plates developed in the fibrous tissue which overlies Meckel's cartilage; these bear teeth, and correspond with the expanded symphysial end of the splenial in *Ceratodus*. *Polypterus* has a true *articulare*, from which Meckel's cartilage is continued. The *angulare* is much shorter, and the *dentale* much longer than in *Ceratodus*.

The hyoidean and opercular apparatus present characters of singular interest. Dr. Günther says that "on the hinder side of the tympanic pedicle,[1] near its base, there is a small round tubercle, for the suspension and articulation of the hyoid arch (Plate XXXIV. fig. 3, *v*)."

I presume that this "small round tubercle" of the suspensorial expansion of the cranium is the small cartilage marked *H.M* in figs. 4 and 6. But this is neither a process of the suspensorium, nor does it articulate with, nor take the principal share in, suspending *Hy*, which is Dr. Günther's "hyoid arch."

In fact it is, as fig. 6 shows, a distinct, though small, four-sided, flattened cartilage, the anterior and ventral angle of which is produced into a short conical process (*Sy*). Its anterior edge is firmly united with the skull, just where the cranium proper passes into the suspensorium. At this point there is a triangular vacuity filled with fibrous tissue, through which the posterior division of the seventh nerve passes (figs. 1 and 6, VII). The outer face of the cartilage is loosely connected with the operculum (*Op*); and the conical process (*Sy*) is embedded in the dorsal and posterior part of the powerful

[1] It is surely to be regretted that any writer of authority should retain the misleading name of "tympanic pedicle" for a part the total distinctness of which from the "tympanic bone" of the higher Vertebrata has now been so copiously demonstrated.

ligament (*h.s*) (corresponding with the hyosuspensorial ligament in *Menobranchus*[1]) by which *Hy* is mainly kept in place.

It is obvious that this little cartilage is the homologue of the hyomandibular element of the hyoidean arch of other fishes, the small conical process being the rudimentary *symplectic*, and, therefore, that it is itself the dorsal element of the hyoidean arch, attached in its normal position, as its relations to the seventh nerve show. The hyoidean cornua are very strong, and consist of a cartilaginous axis almost completely ensheathed by bone. The dorsal end of each is attached by the strong hyo-suspensorial ligament aforesaid to the suspensorium; but another very strong round ligament (answering to the *mandibulo-hyoid ligament* of *Menobranchus*[2]) connects the

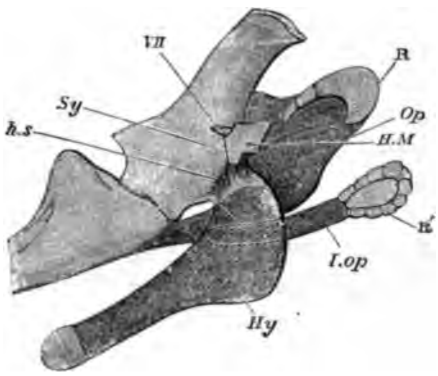


FIG. 6.—*Ceratodus forsteri.* Inner view of the right hyoidean arch (*Hy*), with the opercular apparatus and part of the suspensorium and of the mandible.
H.M. hyomandibular cartilage; *Sy*, its symplectic process; *Op*, operculum; *I.op*, interoperculum; *R*, *R'*, cartilaginous rays attached to the inner face of the operculum and interoperculum; VII, exit of the posterior division of the seventh nerve; *h.s.* hyosuspensorial ligament (immediately beneath it is the mandibulo-hyoid ligament).

dorsal end of the hyoidean cornu with the angle of the mandible (figs. 4 and 6).

Thus the hyoidean arch of *Ceratodus* strikingly resembles that of a Plagiostome on the one hand, and that of an Amphibian on the other. And the small hyomandibular presents a form and connections which are strikingly similar to those of the *suprastapedial* cartilage in the Sauropsida,[3] which, on a former occasion, I showed to be the summit of the hyoidean arch and the homologue of the mammalian incus.

In describing the operculum Dr. Günther says (*l. c.* p. 525), "A small movable piece of cartilage is found inside of the articulary

[1] P. Z. S. 1874, pl. xxix. figs. 1 and 2. [2] P. Z. S. 1874, *ibid.*

[3] 'On the representatives of the Malleus and Incus of the Mammalia in other Vertebrata,' P. Z. S. 1869.

groove of the opercle (Pl. XXXIV. figs. 2 and 3, *k*): it is a rudiment of the præoperculum."

Neither the figures referred to nor the account given enable me to be certain that they apply to the cartilaginous structures I am about to describe, and which are to be found not only on the inner face of the operculum, but on that of the interoperculum.[1]

On the inner side of the former and projecting beyond its free edge is a curved band of cartilage divided into several portions.[2] One of these, that nearest the hyomandibular, is conical and bent at an angle to that which follows it. The terminal plate is broad and crescentic, and, on one side, was subdivided towards its free edge. On the inner face of the posterior end of the interoperculum (*I.op.*) there is an oval cartilage surrounded by eight or nine smaller nodules.

These cartilages represent the cartilaginous branchiostegal rays of Plagiostomes, which are often subdivided into two groups—a dorsal group attached to the hyomandibular, and a ventral group to the cornual division of the hyoid arch.

The *proæperculum* of Fishes and the *squamosal* of the higher Vertebrata are represented by the bone *Sq*, termed "tympanic lamina" by Dr. Günther. I have marked the lower piece, which was distinct on the specimen represented in fig. 4, *Qu*; but in another specimen I can find no subdivision, and I am disposed to think that the division arose from an accidental dismemberment of a squamosal (or præoperculum) corresponding with that of *Menobranchus* (P. Z. S. 1874, Pl. XXIX. fig. 1, *Sq*), and that there is no true quadrate in *Ceratodus*. I can discover no ossification of the substance of the articular extremity of the suspensorium, such as occurs in the Amphibia. The pterygopalatines and the vomers, which last are represented only by the bases of the two vomerine teeth, are similar in their form and relations to the corresponding bones of Urodele Amphibia.

What respect to the branchial apparatus, Dr. Günther (*l. c.* p. 526) says that it "does not differ from that of Teleostean fish, but is

[1] Dr. Günther terms the bone here named interoperculum, "suboperculum." He says (*l. c.* p. 525) that to the lower edge of the operculum "is attached by fibrous tissue the long styliform *suboperculum*, terminating at a considerable distance from the mandibulary joint." It is quite true that the bone in question is thus attached to the operculum; but a much more important connection takes place between its ventral end and the angle of the jaw, by means of strong ligamentous fibres which run into the hyomandibular ligament. It thus more closely resembles the interoperculum of Teleosteans than it does the suboperculum.

[2] In a specimen of the skull of *Ceratodus*, for which I am indebted to my friend Mr. F. M. Balfour, the curved band of cartilage of the operculum is not subdivided, and the interopercular cartilages are divided less regularly and differently on the two sides.

entirely cartilaginous. There are five branchial arches, the last rudimentary and attached to the base of the fourth. There is no peculiar modification of any part of this apparatus; and the middle pieces have the usual groove for the reception of the vessels and nerves."

I find that each of the anterior four branchial arches consists of a long ventral and a short dorsal piece of cartilage: the former pieces are united by ligament at their ventral ends, the third and fourth curving forwards in this part; they are connected by joints surrounded by ligaments with the dorsal pieces (fig. 2). In the median ventral line, between the ends of the ventral pieces, lie two cartilages—an anterior elongated and spindle-shaped (*M.B*[1]), which is connected by a strong ligament with the median piece of the hyoid arch, and a posterior rounded nodule (*M.B*[2]) at some distance from the foregoing. The fifth arch consists of a single piece of cartilage curved forwards and united with the principal branchial of the fourth arch, both above and below; in front of it, close to the ventral end of the fifth arch, was a small nodule of cartilage, which is probably a rudimentary sixth arch (6).

As Dr. Günther has pointed out, the osseous shield which covers the dorsal aspect of the skull consists of two median bones (fig. 7, *A*, *B*), one anterior and one posterior, which he terms "ethmoid" and "scleroparietal," and of two pairs of lateral bones, the "frontals" internally (fig. 7, *C*) and the "tympanic laminæ" externally (fig. 7, *D*). In my specimens the anterior half of the anterior median bone (*A*) has a different shape from that given in Dr. Günther's Plate XXXIV. fig. 1, and its margins are very well defined. Moreover, in one specimen, the hinder end of each inner lateral bone is completed by a distinct ossification (*C'*). There is also a separate ossification (*E*) on the left side, on what corresponds with the front part of the outer lateral bone on the right side. Doubtless these bones are subject to much individual variation.

The fibrous band which extends, below the eye, between the antorbital process and the ventral end of the suspensorium contains three suborbital bones. The anterior of these, trihedral, is connected by its broad base with the antorbital process; the middle bone is slender and elongated; the posterior is broad, flattened from side to side, and its hinder edge is fixed by ligamentous fibres to the outer face of the suspensorium and of the squamosal.

The *basal bone* of Dr. Günther is the parasphenoid. It extends backwards, beyond the limits of the proper cranium, into the region of the vertebral column, to a point just beyond the attachment of the

third pair of ribs. But there is at least one vertebra in front of that which bears the first pair of ribs. In *Ceratodus*, as in the Sturgeon and other Ganoids, several anterior vertebræ have coalesced with one another and with the skull; or, probably, it would be more accurate to say that the investing mass of the notochord has not become differentiated into vertebræ for this extent. Nevertheless the posterior boundary of the skull can be strictly defined by the interspace between

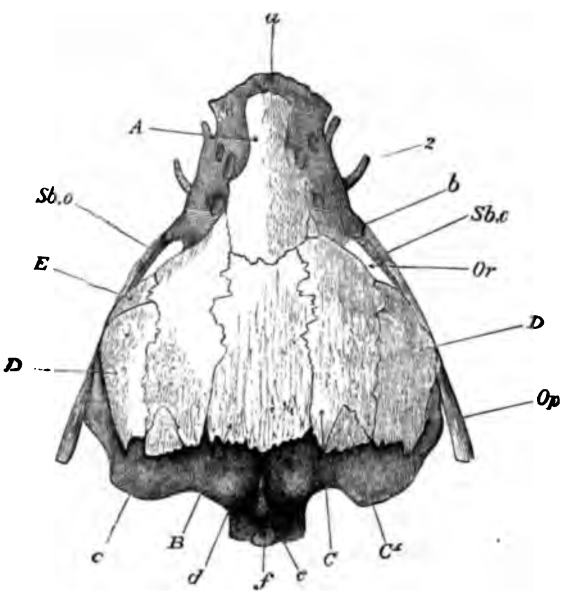


FIG. 7.—*Ceratodus forsteri.* Dorsal aspect of the skull.
a, the anterior end of the chondrocranium; *b*, the antorbital process of the chondrocranium; *c*, its suprabranchial expansion; *d*, lateral elevations of the occiput; and *e*, median ridge, with the surface for the attachment of the anterior fin-ray; *f*, articular surface for the second fin-ray; *A*, anterior median bone; *B*, posterior median bone; *C*, inner lateral bone; *C'*, distinct ossification on the posterior extremity of this bone; *D*, outer lateral bone (squamosal); *E*, a separate ossification on the left side; *Op*. operculum; *Or*, orbit; *Sb.o*, suborbital bones; 2, the posterior upper labial cartilage.

the exit of the pneumogastric and that of the next following, or first spinal, nerve.

It is to the outer surface of this interspace that the anterior edge of the "suprascapular" element of the pectoral arch is fixed by strong ligamentous fibres (fig. 2). Just in front of the boundary between the skull and the vertebral column, and therefore in the side walls of the former, there lies, deep in the substance of the cartilage, a hollow cone of bone (*E.O*). It is wider above and externally than below and internally, where its end lies above the notochord. This appears to be an exoccipital ossification, such as is to be found in

greater state of development in *Lepidosiren*, *Polypterus*, and *Menobranchus*.

The skull of *Ceratodus* is, as might be expected (and as Dr. Günther has pointed out), extremely similar to that of *Lepidosiren*. In fact, beyond differences in the proportions of its various parts, the more extensive fenestration of the roof of the olfactory capsules in *Lepidosiren*, and the absence, so far as my investigations have yet gone, of the hyomandibular cartilage in the latter genus, the cartilaginous elements of the skull are the same in the two cases.

As to the superadded bones, the parasphenoid, the rudimentary vomers, and the pterygopalatine plates correspond in the two genera. The exoccipitals are much larger in *Lepidosiren*. The descending process or præopercular part of the squamosal is best developed in *Lepidosiren*, whilst its dorsal part (proper squamosal) is larger in *Ceratodus*.

In both, there are two opercular bones, an operculum and an interoperculum ; and in *Lepidosiren*, as in *Ceratodus*, there are cartilaginous plates attached to the inner faces of these bones.

The branchial apparatus of *Lepidosiren* differs from that of *Ceratodus* mainly in the greater number of complete branchial arches.

It can hardly be doubted that the bone *D* of *Ceratodus* is represented, though incompletely, by the supraorbital of *Lepidosiren*, while the bony nasal shield of the latter corresponds very closely with the anterior median bone (*A*) of *Ceratodus*. The posterior boundary of the bone, however, lies further back in *Ceratodus* than it does in *Lepidosiren*. The argument of Dr. Günther that the posterior median bone (*B*) in *Ceratodus* is not the homologue of the parieto-frontal of *Lepidosiren*, because it lies above the muscles, while the latter is situated beneath them, is weighty against the identification of the bones in question ; and, in other respects, the parieto-frontal of *Lepidosiren* is very unlike the " scleroparietal " of *Ceratodus*.

When the comparison of the cranial and facial bones of *Ceratodus* with those of the Vertebrata is extended beyond the limits of the Dipnoi, the determination of their homologues is beset with many difficulties. *Polypterus* has an anterior and a posterior median shield in the roof of the skull, which at first seem to correspond with those of *Ceratodus* ; these shields are each formed by the union of two bones, which are evidently comparable to the frontals and parietals of the higher Vertebrata, while the frontals unite with a pair of broad nasals which cover the olfactory sacs. The apices of the posterior triangular edges of these bones reach back to near the level of the middle of the orbits ; and the frontal bones are continued forwards

on each side of them. Between the two nasal bones there is a median ossification which lies upon the mesethmoidal cartilage and spreads out in front, ending by a broad edge which articulates with the præmaxillæ.

The median bone, the piscine "ethmoid," occupies the same position as the anterior median bone of *Ceratodus* would do if the ethmoidal region were reduced to the proportions it has in *Polypterus*. Therefore, from this point of view, the determination of the bone as "ethmoid" by Dr. Günther seems fully justifiable; and the inner lateral and the median posterior bones would seem to represent the frontal and parietal bones of *Polpyterus*.

On the other hand, the many points of resemblance between *Ceratodus* and the Amphibia suggest the comparison of the anterior and posterior median bone to the frontals of *Menobranchus*, and of the inner lateral bones to the parietals of this Amphibian. The forward extensions of the latter, at the sides of the frontals, are specially noticeable in comparison with the anterior extremities of the inner lateral bones of *Ceratodus*. On the whole, I am inclined to think that *Polypterus* is the better guide in the interpretation of the cranial bones of *Ceratodus*, though the difference between the bones of *Ceratodus* and those of the Crossopterygian ganoids, all of which are readily reducible to the Polypterine type, is very considerable.

In other respects the skull of *Ceratodus* finds its closest parallel among the Amphibia, especially such Urodela as *Menobranchus*,[1] and the Anura in their tadpole state.

I have already indicated the chief points of resemblance to the amphibian skull, and need not recapitulate them here. The most important feature is the manner in which the mandibular arch is connected with the skull.

The part of the palato-quadrate cartilage which is united with the skull, between the exits of the fifth and second nerves, answers to the "pedicle of the suspensorium" of the amphibian, while its backward and upward continuation on to the periotic cartilage corresponds with the otic process. As in the Amphibia and in the higher Vertebrata, the mandibular arch is thus attached directly to the skull by that part of its own substance which constitutes the suspensorium. It may thus be said to be *autostylic*.

Among fishes, the only groups which possess an autostylic skull, or in which the dorsal end of the mandibular arch is continuous with the cartilage of the brain-case, are the Chimæroids and the Marsipobranchii.

[1] See P. Z. S. March 17, 1874.

In *Chimæra*, the general form and connections of the palato-quadrate cartilage are the same as in *Ceratodus*; but it differs from that of *Ceratodus* as that of the Tadpole differs from that of a young Frog, or as that of *Menobranchus* differs from that of *Menopoma*; that is to say, the articular condyle is situated far more forward, and the gape is, in consequence, relatively shorter in the former than in the latter. There are the same large olfactory capsules in both cases. In *Chimæra*, however, these project beyond the termination of the ethmoidal cartilage, while in *Ceratodus* the latter projects beyond the olfactory capsules, which are more lateral in position, more elongated, and, in accordance with the general form of the head, much more depressed.

Just as in *Ceratodus*, the palato-quadrate cartilage of *Chimæra* bears two teeth marked with radiating ridges, while two others, the vomerine teeth, are supported by the ethmoidal cartilage in front of these; and in both cases there is a tooth with radiating ridges on its surface in each ramus of the mandible.

In the disappearance of the notochord and the articulation of the skull with the anterior coalesced vertebræ, the skull of *Chimæra* presents a higher degree of differentiation than that of *Ceratodus*; while it is needless to speak of such aberrant peculiarities as its supracerebral interorbital septum, or the vast crest into which the skull is raised above the anterior part of the brain-cavity. In other respects, however, as in the inclination of the axis of the suspensorium already noted, the skull of *Chimæra* presents lower characters than that of *Ceratodus*. Among these may be reckoned the great size of the upper and lower labial cartilages and the condition of the hyoidean arch, which, except in size and some peculiarities of form, is altogether similar to the four branchial arches which follow it. Like them, it terminates, dorsally, in a flat, expanded, triangular piece, which is connected with the superjacent floor of the skull by muscles and ligaments, but by no direct articulation. The dorsal pieces of the succeeding branchial arches have the same form and attachments, and unite with the ventral segments at a sharp angle. These angles are all connected together by a strong ligament, which is continued to the pectoral arch. Moreover a small styliform cartilage passes from the last angle to the pectoral arch, and is connected with the dorsal end of the fifth branchial arch. It appears to represent the dorsal element of that arch.

Johannes Müller, fully appreciating the importance of the differences between the skull of the Chimæroids and those of other "Elasmobranchii," and sagaciously remarking that "the skull of

Chimæra is most like that of a tadpole,"[1] was thereby led to separate the Chimæroids as a suborder of the Elasmobranchii under the name of *Holocephali*. It appears to me that he might have been justified in going still further; for, considering, in addition to the cranial characters, the structure of the vertebral column and of the branchiæ, the presence of an opercular covering to the gills, the peculiar dentition, the almost undeveloped gastric division of the alimentary canal, the opening of the rectum quite separately from and in front of the urinogenital apertures, the relatively small and simple heart, the Chimæroids are far more definitely marked off from the Plagiostomes than the Teleostei are from the Ganoidei.

In all other Fishes, except the Marsipobranchii, the mode of connection of the mandibular arch with the skull is different from that which obtains in the Chimæroids and the Dipnoi. The palato-quadrate cartilage is no longer continuous with the chondrocranium (though the bony elements of that arch may unite suturally with those of the skull, as in the Plectognathi), but is, at most, united with it by ligament. Moreover the dorsal element of the hyoidean arch, or the hyomandibular, usually attains a large size and becomes the chief apparatus of suspension of the hinder end of the palato-quadrate cartilage with the skull. Skulls formed upon this type, which is exemplified in perfection in Ganoidei, Teleostei, and ordinary Plagiostomes, may therefore be termed *hyostylic*.

But though the typical forms of autostylic and hyostylic skulls, as exemplified, *e.g.*, by a Sturgeon, a Pike, and a Dogfish or Ray, on the one hand, and *Chimæra*, *Ceratodus*, and *Menobranchus* on the other, are thus widely different, certain Plagiostomes present a condition of the cranium which tends to connect the two by a middle form, which may be termed *amphistylic*.

In the amphistylic skull the palato-quadrate cartilage is quite distinct from the rest of the skull; but it is wholly, or almost wholly, suspended by its own ligaments, the hyomandibular being small and contributing little to its support. The embryo amphibian is amphistylic before it becomes autostylic; and, in view of certain palæontological facts, it is very interesting that the link which connects the amphistylic with the ordinary Selachian skull is that of *Cestracion* (fig. 8).

If the palato-quadrate cartilage of *Chimæra* were membranous in the centre, as it is in the tadpole, and if along three lines radiating from this centre the cartilage were converted partly into fibrous tissue and partly into a true joint, the result would be to produce a palato-

[1] 'Vergleichende Anatomie der Myxinoiden,' erster Theil, p. 150.

quadrate apparatus such as that exhibited by *Cestracion*. The huge palato-quadrate cartilage (*Pl*, *Qu*) of *Cestracion* is united with the skull in the præorbital region by a joint, and in the orbital region by fibrous tissue, and answers to that part of the palato-quadrate cartilage of *Chimæra* which lies between the nasal capsule and the mandible.

The small cartilaginous plate (*Ot.p*), which is connected only by ligament with the periotic cartilage above and with the quadrate below, answers to the *otic process* of the Frog's suspensorium. This cartilage lies in the front wall of the spiracle, which in *Cestracion* is

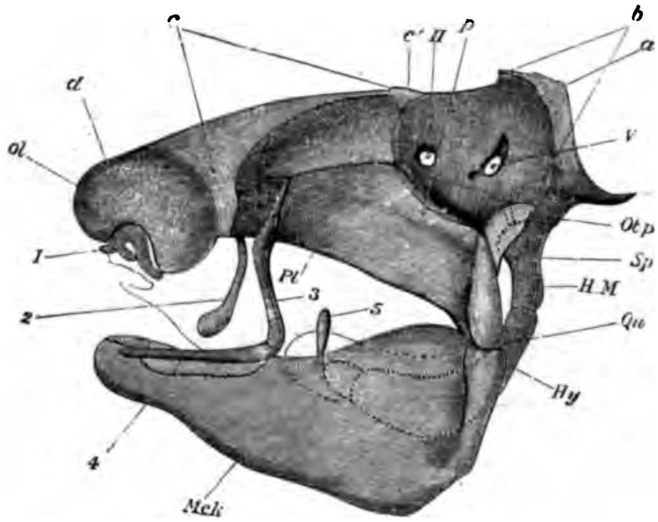


FIG. 8.—*Cestracion philippi.* Left lateral view of the skull.

a, occiput ; *b*, postorbital process ; *c*, *c'*, antorbital process ; *d*, anterior end of the chondrocranium ; *ol*, olfactory capsule ; *Ot.p*, otic process, or spiracular cartilage ; *Sp*, place of the spiracle ; *H.M*, hyomandibular cartilage ; *Qu*, articulation of the palato-quadrate cartilage (*Pl*, *Qu*) with the lower jaw (*Mck*) ; *p*, part of the palato-quadrate arch which answers to the pedicle of the suspensorium in Amphibia ; *Hy*, hyoid ; II, foramen for the optic, and V, for the trigeminal nerves ; 1, 2, 3, 4, the upper and lower labial cartilages ; 5, a small cartilaginous style attached by ligament to the mandibular cartilage.

situated low at the sides of the head, nearly in a line with the branchial clefts, or in the position which it occupies in fœtal Selachians. Moreover this so-called *spiracular cartilage* bears a rudimentary gill and is so far comparable to any of the branchial arches.[1]

In possessing this permanent mandibulo-hyoid cleft, or spiracle, which is the homologue of the tympanic cavity and Eustachian tube of the higher Vertebrata, and in the permanence of its rudimentary branchia, *Cestracion* exhibits a lower stage of organization than *Chimæra*, in which, as in *Ceratodus*, the mandibulo-hyoid cleft has

[1] Gegenbaur considers the spiracular cartilage to be a ray of the mandibular arch.

disappeared. On the other hand, the hyoidean arch presents a form intermediate between that of the ordinary Selachians and that of *Ceratodus* and *Chimæra*. It is stout; and its dorsal element, still retaining a little of its original form, but much thicker and more cylindrical, is no longer united with the skull by ligament and muscle merely, but articulates with a process of the underside of the periotic capsule. Moreover its distal end is connected by strong ligamentous fibres with the posterior end of the palato-quadrate cartilage and with an inward process of the articular end of the mandible (the *sustentaculum* of Gegenbaur).

In fact, the "epibranchial" of the hyoidean arch of *Cestracion* is just beginning to take on a new function, that of suspending the palato-quadrate cartilage and mandible to the skull. It is a true hyomandibular, though small and insignificant relatively to what it becomes in other Plagiostomes, in Ganoids, and in Teleostei.

Had I been acquainted with the skull of *Cestracion* in 1858, I should have been spared the hesitation which I then felt[1] as to identifying the hyomandibular of Fishes with the summit of the hyoidean arch, and which has subsequently been removed by abundant evidence published by Mr. Parker and myself.

In the general form of the skull, the position and proportions of the olfactory capsules, and the characters of the principal labial and alinasal cartilages, *Cestracion* has a stronger resemblance to *Chimæra* than is exhibited by any other Plagiostomes; and I take it to be one of the lowest of Selachian skulls.

I am aware that in expressing this opinion I am diametrically opposed to Gegenbaur,[2] whose elaborate study of the Plagiostome skull entitles his opinion to the greatest weight, and who regards *Cestracion* as possessed of one of the highest of skulls in its group, while *Heptanchus* and *Hexanchus* have the lowest.

There is a certain ambiguity about the terms "highest" and "lowest"; but if by the former we understand the most extreme modification of the hyostylic type of skull characteristic of the group then I should have no hesitation in regarding the skulls of the Rays as the highest of Plagiostome skulls, while *Cestracion* represents a low form of the autostylic type.

[1] 'Croonian Lecture,' 1858, and 'Lectures on the Theory of the Skull,' 1864. See also 'On the Malleus and Incus,' P.Z.S. 1869; 'Manual of Vertebrate Anatomy,' 1871, p. 85; and Mr. Parker's 'Memoir on the Development of the Salmon,' Phil. Trans. 1872.

[2] 'Das Kopfskelet der Selachier,' p. 60. In controverting the opinion of Professor Owen that the *Cestracion* is less advanced in cranial development than *Squatina*, Gegenbaur observes, "So möchte ich gerade das Gegentheil behaupten, und nicht etwan bloss bezüglich der Basalverhältnisse des Craniums."

Notidanus, on the other hand, appears to me to have an essentially low form of skull, so far as it is more completely amphistylic than any ordinary Plagiostome; but on this low form is superinduced a modification by which it approaches the higher autostylic skull. This is the union of the palato-quadrate arch with the postorbital process of the skull—an articulation which, in Prof. Gegenbaur's view, represents the primitive attachment of the mandibular arch, but, in my apprehension, is an altogether secondary connection.

I am indebted to Dr. Günther for a fœtus of *Notidanus* (*Heptanchus*) *cinereus* in excellent condition; and the examination of the skull (fig. 9), which presents all the characteristic features of the adult,[1] has confirmed the suspicion which I previously entertained,

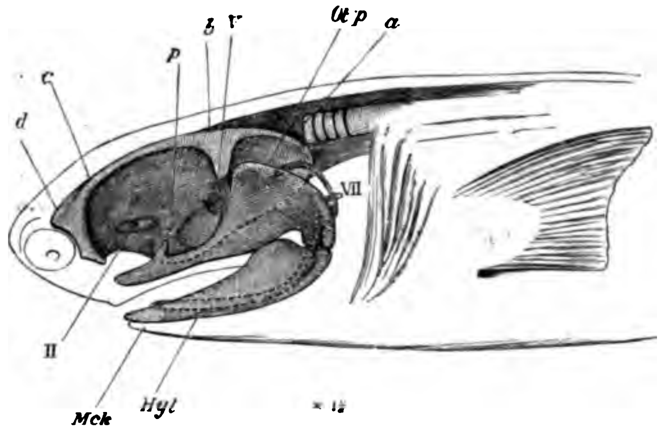


FIG. 9.—*Notidanus cinereus*. Left lateral view of the skull.
Letters as in the preceding figures. VII, the posterior division of the portio dura.

that the skull of *Notidanus*, though fundamentally of a low type, is greatly modified so far as the jaws are concerned. What first led me to suspect that this might be the case was the backward position of the articular end of the suspensorium and the relative length of the gape—features in which the skull of *Notidanus* differs from that of ordinary Selachians as an old frog differs from a young one.

The palato-quadrate cartilage of *Notidanus* has an inward process (*p*), which lies in a strong ligamentous band, by which it is attached to the skull between the optic and trigeminal foramina. This answers to the pedicle of the suspensorium in the Amphibia. From this point the palato-quadrate cartilage extends backwards, as a laterally compressed deep plate, the posterior and inferior extremity of which gives attachment to the mandible. The dorsal and anterior

[1] See Gegenbaur, *op. cit.*

angle of this plate is attached only by ligament to the postorbital process, in the fœtus, but appears to articulate therewith in the adult. I think that there can be no doubt that this upward and backward extension of the palato-quadrate cartilage answers to the *otic process* in the amphibian. It has similar relations to the posterior division of the seventh nerve; and between it and the hyoidean arch lies the spiracle, in correspondence with its homologue the tympano-eustachian passage. The dorsal and posterior edge of this process no less clearly corresponds with the spiracular cartilage in *Cestracion*, otherwise absent in *Notidanus*. The hyoidean arch is attached to the periotic region of the skull. It is very slender; and though closely bound by ligament to the mandibular arch, close to the articulation of the mandible, it can contribute little or nothing to the support of the latter. Remove the great otic process of the palato-quadrate arch of *Notidanus*, and bring its quadrate end further forward, and the result would be a typically amphistylic skull, such as exists in the larval *Siredon* and *Triton*.[1]

The relations of the skulls of *Notidanus*, *Cestracion*, and *Ceratodus* may be thus expressed:—

Notidanus most nearly approaches the amphistylic skull, such as exists in all the autostylic Vertebrata in the embryonic state; but it is considerably altered by the development of a great otic process from the mandibular arch.

In *Cestracion* the palato-quadrate has become massive, and, in the region of the pedicle, is firmly united with the skull, while the otic process is a separate cartilage, connected only by ligament with the postorbital process above and with the palato-quadrate below.

In *Ceratodus* the palato-quadrate has coalesced with the skull both by its pedicle and by its otic process; and the same change occurs in the autostylic skulls of the Amphibia.

In the ordinary Plagiostomes, on the other hand, the palato-quadrate becomes smaller and more freely united with the skull. The otic process (=spiracular cartilage) is smaller, and the hyomandibular takes a larger and larger share in suspending the mandibular arch to the skull, which is therefore eminently hyostylic.

Turning now to osseous fishes, the skull which presents the nearest resemblance to *Ceratodus* is that of *Polypterus*. This will be obvious to any one who studies the excellent description of the chondrocranium of this fish given by Dr. Traquair.[2]

But in the character of the palato-quadrate arch and the great

[1] P. Z. S. 1874, pl. xxxi, figs. 1 & 2.

[2] 'The Cranial Osteology of *Polypterus*,' Journal of Anatomy and Physiology, 1870.

relative size of the hyomandibular, the skull is as thoroughly and completely hyostylic as is that of any other existing Ganoid or Teleostean.

Thus, having regard only to the structure of the cranium, the relations of *Ceratodus* may be expressed as follows:—

Amphibia.		*Ganoidei.*	*Teleostei.*
CERATODUS.	*Cestracion.*		*Raia.*
Chimæra.	*Notidanus.*		
AUTOSTYLICA.	AMPHISTYLICA.	HYOSTYLICA.	

III. *The Pectoral Limb.*

In the memoir cited, Dr. Günther describes the limbs of *Ceratodus* and their skeleton as follows:—

"The limbs consist of two pairs of paddles, similar in appearance to the termination of the tail; viz. a longitudinal axis, formed by the endoskeleton and muscles and covered with scales, is surrounded by a broad rayed fringe. These paddles are structurally identical with the fins of *Lepidosiren*; only the axis and also the fringe are much dilated. The pectoral and ventral paddles taper to a fine point, the former being longer than the head, the latter rather shorter. The ventral paddles are inserted at a short distance in front of the vent" (p. 515).

"The paddle is joined to the scapular arch by an elongate, flattish, slightly curved cartilage: its proximal end has a glenoid cavity, fitting into the humeral condyle; the joint is simple, free, allowing of a considerable amount of motion, its parts being held together by a ligament fastened round its circumference. This is the only true joint in the limb, all the other parts being fixed to one another by connective tissue. I consider this cartilage to be the forearm; a horizontal section along its longitudinal axis does not show any primary division. The next following cartilage forms the base of the paddle; although externally it appears as a single flat, broad, short piece, unevennesses of its surface indicate that several primary pieces are coalesced in it.

"I am confirmed in this view by a horizontal section, in which the lines of the former divisions are preserved in the shape of tracts of a white connective tissue. Three such divisions may be distinguished, corresponding to the three carpals of most Plagiostomes.[1]

[1] Pro-, meso-, and metapterygium of Gegenbaur.

If this determination is correct, then the antibrachial cartilage just described is not represented in that order.

"The remaining framework of the paddle shows an arrangement unique among the Vertebrata. From the middle of the basal cartilage a series of about twenty-six subquadrangular pieces takes its origin, forming a longitudinal axis along the middle of the paddle to its extremity. The pieces become gradually smaller, and are scarcely distinguishable towards the end of the paddle. On the two posterior corners of each piece a branch is inserted, running obliquely backwards towards the margin of the fin; the branches of the first eight or twelve pieces are three-jointed, the remainder two-jointed, the last having no branch at all. Slight irregularities, such as the origin of two branches from one side of a central piece, occur, as also several four-jointed branches being inserted immediately on the basal cartilage" (pp. 532–3).

In general, this description suits the pectoral fins of the specimen I have described very well. Mine, however, has only twenty median cartilages. All but the very last bear lateral rays; but towards the distal end of the fin these become minute, and consist of a single piece. Moreover the distal joints are much more slender, especially the last. A more important point is that the second shows no trace of such divisions as those described by Dr. Günther. To make sure of this I made a thin microscopic section of this cartilage on the right side, and thereby satisfied myself of the homogeneity of the cartilage of which it is composed.

I find no true joint between the proximal median piece and the scapular arch, the connection between the two being effected by a solid fibrous mass.

Again, the "slight irregularities" in the distribution of the rays, in respect of the median pieces, of which Dr. Günther speaks, are constant peculiarities of no small importance. This becomes obvious when the fin of *Ceratodus* is compared with that of other fishes. But before proceeding to this point I must make a few remarks on the normal and primitive position of the vertebrate limb, and on the changes from that normal position which take place in fishes on the one hand, and the higher Vertebrata on the other, as, for want of attending to this fundamental matter, grave errors have crept into the interpretation of the parts of the limbs of different vertebrates.

The fins occupy the normal position in such a fish as *Scyllium*. When the axis of the body is horizontal the plane of the fin is also horizontal. Its upper surface is covered by a continuation of the dorsal integument, and its lower surface by that of the ventral side

of the body. The distinctive spotting of the dorsal aspect in the Dogfish makes this very plain; therefore, to adopt the nomenclature which I some time ago proposed, the convex thick edge of the fin is præaxial, while its concavo-convex thin edge is postaxial, and its two aspects look respectively upwards and downwards.

In *Ceratodus*, however, the fin has undergone a rotation upon its axis, in virtue of which its proper ventral surface looks more or less outwards, and its proper dorsal surface more or less inwards; and at the same time the præaxial edge is turned upwards, while the postaxial edge is turned downwards. This is very marked when the fin is applied to the trunk; but the primitive disposition of the surfaces and edges of the limb becomes obvious when the fin is made to stand out at right angles to the axis of the body.

In *Acipenser*, as in any Teleostean fish, the rotation becomes still more marked; and divarication of the fin does not greatly diminish it, by reason of the articulation of the præaxial fin-ray with the pectoral arch at a point higher than the proper glenoid cavity.

When *Ceratodus*, or a Teleostean fish, is placed side by side with a Urodele Amphibian, such as *Menobranchus*, in which the fore limb naturally takes a position nearly parallel with the axis of the trunk, the manus being directed backwards, nothing is more natural than to imagine that the outer and inner aspects and the dorsal and ventral edges of the two correspond.

But a very little consideration will show that nothing can be more erroneous; for the outer surface of the *Menobranchus* limb is its proper dorsal aspect, and the inner surface is its ventral aspect, as will be seen the moment the limb is placed at right angles with the trunk. In fact, though in the amphibian, as in the fish, the limb has undergone a twist, the direction of its rotation is exactly contrary to that which has occurred in the fish. Taking the left limb in each case, the normal fin would have to be turned in the direction of movement of the hands of a watch to bring it to the teleostean position, while it would have to be turned in the contrary way to bring it into the amphibian position. Hence the præaxial edge in the teleostean fin is dorsal, while in the amphibian limb it is more or less ventral; and the skeletal elements on the dorsal side of the axis of the fish-fin answer to those on the ventral side of the axis in the amphibian limb.

As Dr. Günther has observed, the contour of the fin in *Ceratodus* is somewhat like that of a sickle. The præaxial edge is convex forwards and rather thicker, especially at its proximal end, than the posterior edge, which is concave backwards in its distal and convex

in its proximal half. The apex of the fin is slender and recurved. A rounded and narrowed neck unites the limb with the trunk.

Thus the limb, as a whole, is essentially unsymmetrical when its postaxial and præaxial halves are compared. A corresponding asymmetry is strikingly obvious in the skeleton when it is prepared

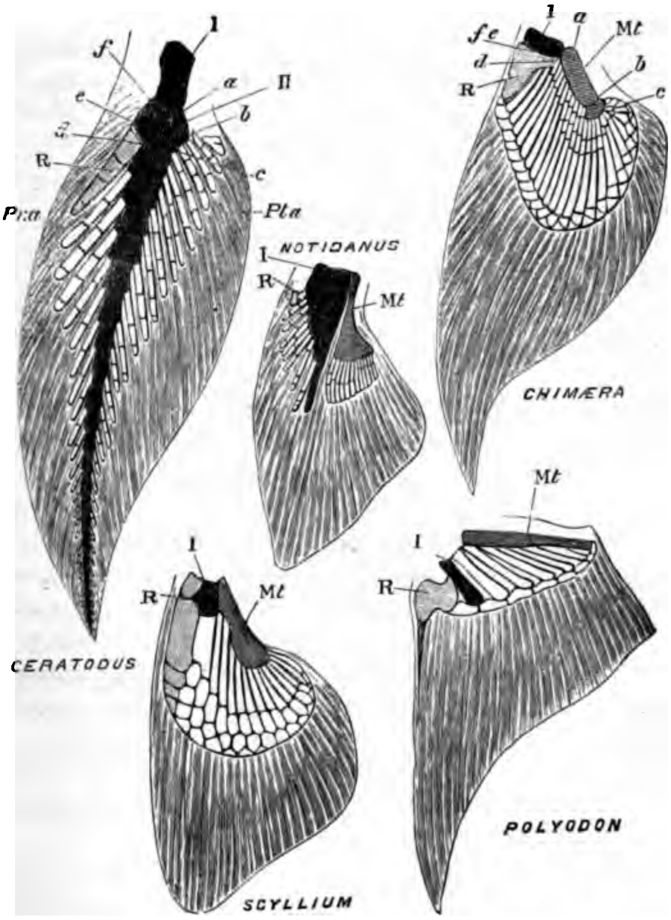


FIG. 10.—The left pectoral fins of *Ceratodus forsteri*, *Notidanus cinereus* (fœtal), *Scyllium canicula*, *Chimæra monstrosa*, and *Polyodon folium*.

The præaxial (*Pr.a*) and postaxial (*Pt.a*) margins of all are turned in the same direction; *R*, the præaxial ray (propterygium of Gegenbaur); *Mt*, the metapterygium; I, the basal or proximal joint of the axial skeleton.

by removing the integument and muscles of the dorsal face, while the undisturbed condition of the parts is preserved by leaving the ventral integument and muscles untouched (fig. 10).

It will be seen that, on the præaxial side (*Pr.a*), each of the sub-

quadrate segments of the median part of the skeleton, except the first and the terminal segments, gives attachment by its distal angle to a single jointed ray. The proximal or first ray (*R*) is much stouter than any of those which succeed it; and all take a direction approximately parallel to one another, their long axes forming an acute angle with that of the series of median segments. In the distal portion of the fin, the postaxial rays have a similar arrangement, and are only more slender than the præaxial rays. But the second segment bears no fewer than five rays. Of these, the proximal, which is shortest and slenderest, stands out at right angles to the axis of the series of median segments; while the others are gradually inclined at a less and less angle to it. The third segment and the fourth each carry two postaxial rays; the rest have but one.

Dr. Günther's figures show that, in his specimen also, the fourth and the third segments each bore two postaxial rays; but there are only four attached to the second segment, and all these are represented as if they had nearly the same inclination to the axis of the fin as the præaxial rays.

To dwell so strongly upon these minutiæ may seem to be making a great deal of a very small matter; but its importance becomes manifest when the fin of *Ceratodus* is compared with that of other fishes.

In my "Preliminary Essay on the systematic arrangement of the Fishes of the Devonian epoch,"[1] I made use of the term "Crossopterygian" to express a peculiarity which is very strikingly manifest in the fishes to which I applied it, the fin-rays of the paired fins being disposed, like a fringe, round an oval, or elongated, central space covered with scales. The Crossopterygii, however, were not defined by this character alone; and hence the fact that truly fringed fins are found beyond the limits of that group does not interfere with its perfectly natural character. In strictness, all fishes which possess paired fins are Crossopterygian in so far as the fin-rays always fringe the edges of the fin; and they differ only in the relative extent of the central area, on which the fin-rays do not encroach.

All the Chimæroids and Plagiostomes are eminently crossopterygian so far as their fins are concerned; and therefore we might expect to find in the skeleton of the pectoral fins of these fishes a modification of the skeleton of that of *Ceratodus*. But in most of these fishes the skeleton of the fins has undergone such an amount of metamorphosis that it is difficult to reduce it to the type of

[1] 'Memoirs of the Geological Survey of the United Kingdom,' decade x. 1861.

Ceratodus. In *Notidanus*,[1] however, the skeleton of the pectoral fin affords the key to the nature of this metamorphosis. Here (fig. 10) there is an axial cartilage, the broad proximal end of which articulates with the pectoral arch. Distally it diminishes in diameter, and ends by a truncated face, with which another slender cylindrical cartilage, also axial in position, is articulated.

I take these two cartilages to represent the shrunken axis of the fin of *Ceratodus.* The præaxial basal angle of this axial mass is occupied by a distinct cartilage. Whether this represents the proximal axial cartilage of *Ceratodus*, or whether it is the proximal præaxial ray, is not clear.

The præaxial edge of the principal axial cartilage, at some little distance from this piece, presents a series of notches, with which are articulated a corresponding number of præaxial rays, while, as has been already stated, a single ray is articulated to the base of the terminal axial cartilage. The uppermost or proximal præaxial ray is two-jointed and broader than the others. On the postaxial side there is a triangular cartilage (*Mt*), wide distally, very narrow proximally, where it is connected with the proximal end of the axial cartilages. Twelve postaxial rays are articulated with the wide distal edge of this cartilage. I conceive that this triangular postaxial cartilage is formed by the coalescence of the axial ends of the postaxial rays.

The fin skeleton of *Notidanus* thus results, in the simplest possible manner, from the shortening of the axis of such a fin-skeleton as that of *Ceratodus* and the coalescence of some of its elements.

In *Cestracion* (fig. 11) the same process is carried a step further Here there is a large cartilage (I) which articulates with the pectoral arch by a concave facet, and corresponds with the proximal axial cartilage of *Ceratodus* and *Notidanus.* United by ligament with its hinder concave margin is the triangular postaxial cartilage (*Mt*), which obviously answers to the similarly shaped postaxial cartilage of *Notidanus*, and which bears a series of postaxial rays, of which the first is directed almost at right angles to the axis of the fin, as in *Ceratodus.* The first præaxial ray (*R*) is very large and bifurcates distally. The ray which is attached to the distal angle of the axial cartilage probably answers to the ray-like termination of the axial skeleton in *Notidanus* ; but it is not distinguishable from the rest.

In the Dogfish (*Scyllium*) (fig. 10) the further shortening of the axis gives rise to still greater changes. The axial cartilage (*meso-*

[1] The figure represents the fin of the fœtal *Notidanus* to which I have already referred. The figure of the fin of an adult of the same species given by Gegenbaur (' Untersuchungen,' Heft ii. Taf. ix. fig. 2) shows essentially the same structure.

pterygium of Gegenbaur (I) is relatively small; but the enlarged postaxial cartilage (*metapterygium, Mt*) has extended upwards along the postaxial face of the first, until it has not only reached the articular surface of the pectoral arch, but furnishes a large part of the articular

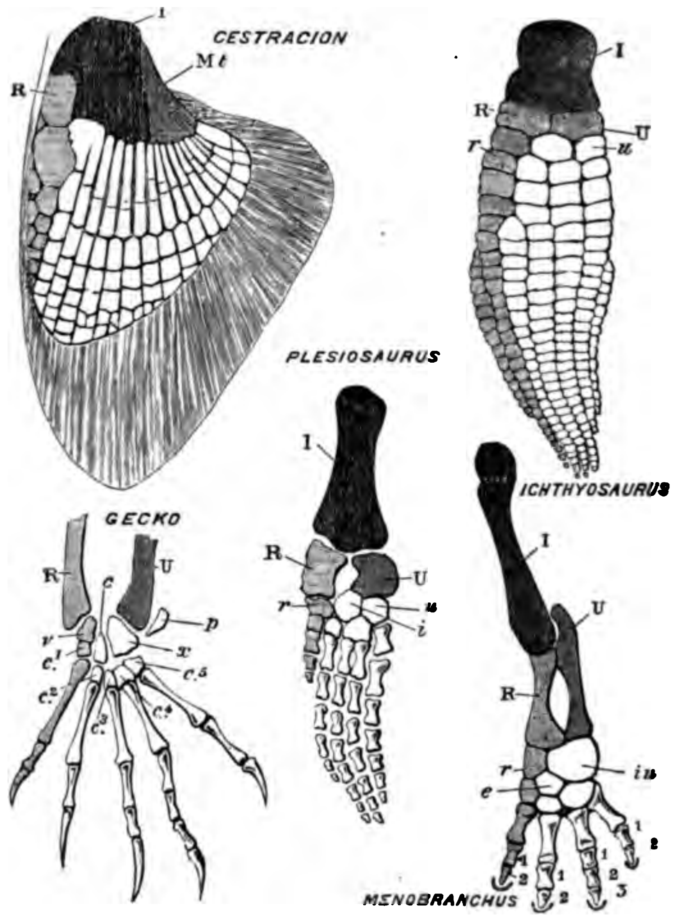


FIG. 11.—The left pectoral fin of *Cestracion philippi* (letters as before), the left fore limbs of *Ichthyosaurus, Plesiosaurus, Menobranchus*, and the left manus of *Gecko verus*.

I, humerus; *R*, radius; *U*, ulna; *r*, radiale; *i*, intermedium; *u*, ulnare; *c*, centrale; c^1, c^2, c^3, c^4, c^5, distal carpals; 1, 2, 3, phalanges of *Menobranchus*. In *Gecko* it is uncertain whether *x* represents the intermedium and the ulnare coalesced as in *Menobranchus* (*i u*), or whether *x* is the intermedium and *p* is the ulnare, occupying the place of a pisiform bone.

cavity. In like manner the proximal præaxial ray (*propterygium, R*) has ascended along the præaxial face of the axial cartilage, until it also is able to furnish a facet which completes the anterior part of the cup for the condyle of the pectoral arch.

In *Squatina*, similar modifications have occurred; but the axial cartilage remains large, and the large præaxial and postaxial cartilages are directed respectively forwards and backwards, in accordance with the form of the vastly expanded fin.

In *Raia*, yet further expansion is obtained by the separation of the axial and postaxial cartilages and the interpolation of postaxial rays between them. The proximal ends of these enter into the articulation, as the great postaxial cartilage had already done.

The interpretation of the skeleton of the pectoral fin of *Chimæra* presents some difficulties. This skeleton consists (fig. 10) of:—(1) a proximal cartilage (I), which articulates by an excavated surface with the condyle of the pectoral arch; (2) a flat, curved, elongated middle cartilage (*Mt*), which is inclined backwards; (3) a small semilunar distal cartilage (*c*), which fits on to the convex distal end of the last. At the end of the convex posterior edge of the distal cartilage is a small cartilaginous ray, consisting of a long basal and a short terminal segment. Similar rays, which gradually become longer, follow this along the free convex edge of the distal cartilage and that of the middle cartilage; but the proximal end of the latter bears a much stronger ray, with a wide base (*R*), which for the most part unites with the ventral edge of the proximal cartilage (I), but is connected with the middle cartilage (*Mt*) by its posterior produced angle.

There can, I think, be no doubt that the proximal cartilage (I) in *Chimæra* answers to the proximal cartilage in *Ceratodus*. The small proximal postaxial cartilages also exactly correspond; and the large proximal præaxial rays no less closely answer to one another. But if this be so, it follows that the whole skeleton of the fin in *Ceratodus* is represented in that of *Chimæra*. The distal cartilage (*c*) in *Chimæra* is the result of the coalescence of the bases of a certain number of the postaxial rays, as is obvious on tracing the series round.

Hence it would appear that all that can represent the series of median segments except the first is the middle cartilage (*Mt*). It further seems probable that this middle cartilage in great part if not wholly, represents the second segment of the *Ceratodus* limb. The postaxial edges, *a b* and *b c*, correspond closely; but the edge *e f*, long in *Ceratodus*, is reduced to nothing in *Chimæra*; while the edge *c d*, occupied exclusively by the third segment in *Ceratodus*, is greatly elongated and bears all the præaxial rays in *Chimæra*.

In order to change the skeleton of the pectoral fin of *Ceratodus*

into that of *Chimæra*, all that will be necessary, if this comparison is correct, is that the third and following median segments of the former shall be gradually reduced, either by abortion or coalescence with the second, more and more postaxial fin-rays becoming attached to the postaxial edge of the second segment, and more and more of the præaxial rays to its præaxial edge. At the same time the first præaxial ray, enlarging backwards and forwards, intercepts the proximal ends of two or three of the following rays, and comes into connection with the proximal segment.

The difficulty which arises out of this apparently natural interpretation of the parts of the skeleton of the fin of *Chimæra* consists in this—that it leads to a doubt as to the true nature of the postaxial cartilage (*Mt*) in *Scyllium*, and therefore in other Plagiostomes. For this metapterygial cartilage cannot at the same time represent coalesced postaxial rays, as the analogy of *Notidanus* would suggest, and the second joint of the axial skeleton, as the analogy of *Chimæra* on the interpretation just given, indicates. If, following the analogy of *Notidanus*, we consider *Mt* in *Chimæra* to be formed of coalesced postaxial fin-rays, then the structure will present no difficulty, but will come very near that presented by the fin of *Cestracion*. The study of the development of the parts can alone solve this problem; but I am inclined provisionally to adopt the latter hypothesis, plausible as the former seems.

Polypterus and *Polyodon* furnish the best connecting links between the Plagiostome fin and that of the other Ganoidei and the Teleostei. In *Polypterus* the *Scyllium* type is essentially preserved. In *Polyodon* and all other Ganoids of which the fin-structure is known, the type is essentially that of the Rays, in so far as fin-rays enter into the glenoid articulation behind the proximal median segment (I). These and many other special modifications of the fish's fin have been carefully worked out by Gegenbaur,[1] to whose excellent descriptions I have nothing to add.

If the interpretation which I have here endeavoured to make good is correct, it is clear that, as Gegenbaur has suggested, *Ceratodus* presents us with the nearest known approximation to the fundamental form of vertebrate limb, or *archipterygium*. But the asymmetry of the skeleton of the fin of *Ceratodus*, and the differences between its distal and its proximal portions, as well as the fact that the proximal median segment has no rays, appear to indicate that the veritable *archipterygium* has undergone a certain amount of modification even in *Ceratodus*. Analogy leads to the suspicion that a still more

[1] 'Untersuchungen,' Heft ii. 'Brustflosse der Fische,' 1865.

archaic fish than *Ceratodus* would have as many pairs of rays as median pieces. In this condition the skeleton would be made up of homologous segments, which might be termed *pteromeres*, each of which would consist of a *mesomere* with a præaxial and a postaxial *paramere*. And as this is the actual state of a great portion of the skeleton of the fin in *Ceratodus*, it may perhaps be permissible to carry speculation as to the primitive condition of the vertebrate limb thus far. Dr. Günther and Professor Gegenbaur go a step further, and suggest that even this *archipterygium* may be the secondary product of the coalescence of many longitudinal cartilaginous elements, which are united by their bases, while they fray out, as it were, at regular intervals towards the distal end of the limb. In this case, Gegenbaur has most ingeniously suggested that the pectoral arch, with its limb, would correspond with a branchial arch and its rays.

It will be observed that the view of the special homologies of the elements of the skeletons of the fins of fishes which I have ventured to put forth differs, fundamentally, both from that suggested by Dr. Günther and from that advanced by Gegenbaur, either in its original form or as he has modified it subsequently to the discovery of *Ceratodus*.

The former says (*l. c.* p. 533):—"When I designated the arrangement of the parts of this pectoral skeleton unique, I did not mean to convey the idea that no homological relation could be pointed out between the parts of the pectoral skeleton of *Ceratodus* and that of other fishes. It is quite evident that we have here a further development of the simple pectoral axis of *Lepidosiren* in the direction towards the Plagiostomes. The pectoral skeleton of *Lepidosiren paradoxa* consists merely of the central series of cartilages of *Ceratodus*; there is no fin-like expansion of the skin of the pectoral limb, which is a simple tapering filament. In *Lepidosiren annectens* this pectoral filament is bordered by an expansion of the skin along its lower edge; and even minute fin-rays are imbedded in each lamina of the fold; in order to support this low, one-sided, rayed fringe, very small, single-jointed cartilages are added to the axis.[1] The fin is still more developed in *Ceratodus*: it has become a broad, scythe-shaped paddle, dilated by a fold of the skin, with two layers of fin-rays surrounding it in its entire circumference; therefore supporting cartilaginous branches are added on both sides of the axis; and most of the branches are composed of several

[1] Four or five of these ray-bearers are obliquely attached to each joint of the axis (Peters, Müller's 'Archiv,' 1845, Taf. 2. fig. 2)

joints, in order to reach the more distant parts which require the support."

This is the exact converse of the view of the relations of *Lepidosiren* and *Ceratodus* which, in agreement with Gegenbaur, I am disposed to take. The fin of the former appears to me to be a reduced and metamorphosed state of the more primitive condition retained in *Ceratodus*.

Dr. Günther goes on to say that "the arrangement of the limb-skeleton of *Ceratodus* is foreshadowed in the pectoral fin of *Acipenser*." On the contrary, in my judgment, the pectoral fin ot *Acipenser* has been derived by much modification from a *Ceratodus*-like type.

In referring to those points in which I venture to dissent from Professor Gegenbaur's interpretation, I cannot refrain from expressing my sense of the very great value of his investigations into the morphology of vertebrate limbs, and my grateful indebtedness to the rich fund of new facts and new ideas which they contain. However, I found myself unable fully to accept his theory of the fish's fin and the vertebrate limb generally, in its original form ; and I expressed my hesitation and its grounds in the German version of my 'Manual of the Vertebrata.'[1] Gegenbaur's later view is concisely stated in his 'Grundriss der vergleichenden Anatomie,' 1874, p. 493, in the following words :—

"The very various forms of the skeleton of the free limbs are deducible from a fundamental form of which only a few instances remain, and which, as representing the first and lowest condition of the fin-skeleton, I term the *archipterygium*. This is represented by a jointed cartilaginous *stem*, articulated with the pectoral arch and giving attachment, on each side, to a series of likewise jointed pieces, the *radii*. The whole structure, resembling a pinnate leaf, is singularly like the supporting apparatus of many Selachian gills, and thus throws a gleam of light upon the phylogeny of the limbs.

"*Ceratodus* presents this form of fin-skeleton, which was perhaps usual among the *Crossopterygidæ*, at present represented only by *Polypterus*. The biserial rays of the fin undergo different modifications. Among the Dipnoi the medial [postaxial] rays are retained in the form of thin rods of cartilage ; while in the Selachians the lateral [præaxial] rays attain a considerable development and constitute the greater part of the massive fin-skeleton. Of the medial [postaxial] rays but few remain, though they are sufficiently distinct

[1] 'Handbuch der Anatomie der Wirbelthiere,' übersetzt von Dr. F. Ratzel (Breslau, 1873), pp. 34, 35.

to sanction the assumption of a former more extensive biserial arrangement of rays on the stem of the fin."

The *metapterygium* Gegenbaur considers to answer to the axial skeleton of the *archipterygium*. The *propterygium* is formed by the union of the proximal præaxial fin-rays. The *mesopterygium* is formed by a certain number of the succeeding præaxial fin-rays.

The only part of this interpretation with which I can agree is the determination of what Gegenbaur names the propterygium as the representative of the proximal præaxial fin-ray or rays in most cases, but not in *Chimæra*, and probably not in *Notidanus*.

In my judgment, the mesopterygium of Gegenbaur is the proximal piece of the axial skeleton, which constantly retains its primary articulation with the pectoral arch. His propterygium represents the proximal præaxial fin-ray, and his metapterygium the proximal postaxial fin-ray, in almost all cases; and the *ichthyopterygium*, as the typical fish-fin may be termed, differs from the archipterygium not by the more or less complete suppression of the postaxial rays, but by the general abbreviation of the whole skeleton and the gradual connection of more or fewer fin-rays (*parameres*) with the pectoral arch.

In the effectual discharge of the function of the fish's fin, increase of breadth is needed; and this increase of surface is obtained by the gradual approximation of more and more lateral elements of the archipterygium to the shoulder-girdle.

Professor Gegenbaur has extended his theory of the limbs to the higher Vertebrata. He conceives that the axis of the archipterygium (which he considers to be the homologue of the metapterygium of the Selachian) is represented by the series of bones which is formed by the humerus, the radius, the radial segments of the carpus, and the radial digit or pollex; while the ulna, the radial segments of the carpus and the ulnar digit, the other carpal bones, and the fourth, third, and second digits represent so many præaxial rays. The very serious objection that this hypothesis makes the radius and the radial digit postaxial, while, as a matter of fact, in every vertebrate animal it is præaxial, is met by the assumption of a torsion of the humerus. But I must confess that I am wholly unable to satisfy myself of the existence of any torsion of the humerus capable of bringing about the effect attributed to it in any vertebrated animal; and, moreover, if such torsion has brought about the observed position of the manus and pes in the higher Vertebrata, any reversal of that torsion would destroy the homology of the pollex and the hallux—which is surely out of reach of doubt.

I am disposed to think, though I am far from imagining that the hypothesis can at present be demonstrated, that the higher vertebrate limb has arisen from the archipterygium in another and simpler method.

According to Gegenbaur's view, the higher vertebrate limb is the result of further progess, in the same direction, of the metamorphosis which has given rise to the ichthyopterygium. But this appears to me to be highly improbable. The ichthyopterygium is specialised *pari passu* with the other peculiarities of piscine structure, and is not developed in the Dipnoi, which are the nearest allies of the Amphibia. Moreover the higher vertebrate limb, which may be termed the *chiropterygium*, as an organ of support and prehension, requires length, strength, and mobility of its segments—conditions exactly the opposite of those which give the ichthyopterygium its special utility.

Hence, as the most highly specialised forms of ichthyopterygium result from the shortening of the skeleton of the fin, the approximation of its distal elements to the shoulder-girdle, and the multiplication of its rays, we might expect that the chiropterygium would take its origin by the lengthening of the axial skeleton, accompanied by a removal of its distal elements further away from the shoulder-girdle, and by a diminution in the number of the rays.

The parts which are traversed by a line drawn through the humerus, the intermedium, the centrale, the third distal carpal, and the third digit in the cheiropterygium may be regarded as so many mesomeres, representing the axis of the archipterygium. Two pairs of parameres are retained on each side. The præaxial are:—(1) the radius, the radiale, the first distal carpal, and the pollex; (2) the second distal carpal and the index. The postaxial parameres are:—1) the ulna, the ulnare, the fifth distal carpal, and the digitus minimus; (2) the fourth carpal and the annularis.

In fig. 11 the skeleton of the pectoral fin of *Cestracion* is represented side by side with the skeleton of the fore limbs of *Menobranchus*, *Ichthyosaurus*, *Plesiosaurus*, and *Gecko*; and the shading of the different parts of the ichthyopterygium is repeated in what I suppose to be the homologous elements of the chiropterygium. In the case of *Menobranchus*, however, it is possible that the true pollex is suppressed, and that the actual radial digit represents the second of the pentadactyle limb, and therefore should have been left unshaded.

In accordance with the view thus suggested, the humerus in the chiropterygium is the homologue of the proximal mesomere or joint

of the axis of the archipterygium, while the radius and the ulna are the homologues of the proximal ends of præaxial and postaxial parameres of the archipterygium.

The confirmation or refutation of this hypothesis is to be sought in development, and in the condition of the limbs in those Palæozoic Amphibia which may have more nearly approximated to Dipnoi than any existing or extinct forms at present known. I suggest it mainly in the hope of stimulating investigation in both these directions.

IV. *Taxonomy of* Ceratodus, *and Remarks on the Classification of Fishes.*

The indications afforded by the brain, the skull, and the limbs of *Ceratodus* are sufficient to show that it occupies a curiously central position among the Ichthyopsida, being allied on one side to the Amphibia, on another to the Chimæroidei and Plagiostomi, and on yet another to the Ganoidei—especially to that group of the Ganoids which I have termed *Crossopterygidæ*, and to the affinities of which with *Lepidosiren* I called attention in 1861.

But even *Dipterus*, which approaches *Ceratodus* and *Lepidosiren* so closely in its dentition and in the form of its fins, is far more similar to *Polypterus* and *Amia* in other respects ; and there is, at present, no reason to believe that any of the Crossopterygian Ganoids possessed other than a hyostylic skull, or differed from *Polypterus* in those respects in which *Polypterus* differs from the existing Dipnoi. All known Crossopterygians have jugular plates, of which there is no trace in the Dipnoi. And as to the position of the anterior nares, which appear to have been situated on the under face of the broad snout, not only in *Dipterus*, but in *Osteolepis* and *Diplopterus*, I have shown above that, so far from being a diagnostic character of the Dipnoi, it is simply an embryonic feature retained in them, the Selachians, and very probably in many of the early Ganoidei. On the other hand, in *Amia*, there is an even closer approximation between the Ganoids and the Teleosteans than can at present be shown to exist between any Ganoids and the Dipnoi ; while the differences between the Dipnoi and the Chimæroidei, and between the Chimæroidei and the Plagiostomi respectively, are not less than those between the Ganoids and the Dipnoi.

It seems to me, therefore, that by forming the Dipnoi, Ganoidei, Chimæroidei, and Plagiostomi into a group of " Palæichthyes," from which the Teleostei are excluded, as Dr. Günther proposes to do, the

differences between the Teleostei and the other hyostylic fishes are brought into undue prominence, and that it is better to retain the Müllerian groups of Dipnoi (*Cirenoidei*, Müller), Ganoidei, Teleostei, Plagiostomi, and Chimæroidei (*Holocephali*, Müller) as equivalent and distinct natural assemblages.

In discussing any system of classification, however, it must be recollected that known forms certainly represent but a portion, and probably a small portion, of those which have existed, and that the most natural groups are therefore, to a great extent, the result of the influence of extraneous, and what may be properly termed accidental, conditions.

It has occurred to me that, in the present state of science, it is very desirable to have some mode of stating the facts of morphology in a condensed and comprehensible form, which shall be purely objective and free from speculation; and I now proceed to illustrate my meaning by drawing up a scheme of the morphology of the Ichthyopsida.

Looking at the animals included under this head as a whole, or at the development of any of the higher members of the group, it is observable that they present a certain series of stages of differentiation marked by the broad characters of the skull, the nature of the olfactory and respiratory organs, and the development or non-development of an opercular fold of the integument.

Thus the skull either retains its primitive segmentation (*Entomocrania*), or the primitive segmentation is lost, and a chondrocranium is developed (*Holocrania*). There are two external nostrils (*Amphirhina*) or only one (*Monorhina*).

A *pneumatocœle*, or air sac, which may become either an air-bladder or a lung, is developed (*Pneumatocœla*), or not (*Apneumatocœla*); and a fold of the integument may cover the branchial apertures (*Operculata*), or not (*Inoperculata*).

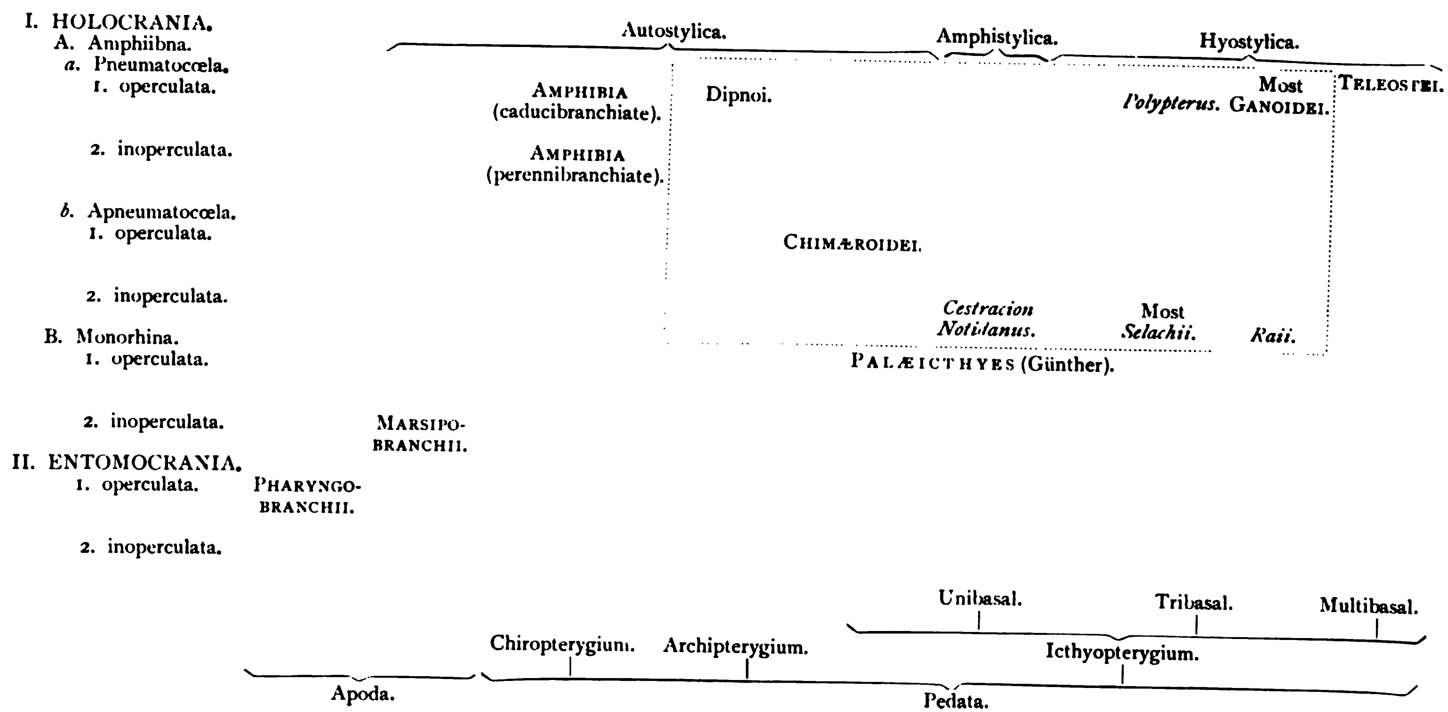
The Ichthyopsida also exhibit a series of stages of differentiation of the limbs, being either apodal or pedate: and, when pedate, having the limb-skeleton constructed upon the type of the archipterygium, or on that of the ichthyopterygium, or on that of the chiropterygium.

Moreover, when the limb is an ichthyopterygium, it may possess one, or at most two basal elements, which articulate with the pectoral arch (unibasal), or there may be three (tribasal), there may be many (multibasal), in accordance with the greater and greater divergence of the fin from the archipterygial type.

The chondrocranium may be constructed upon either the amphistylic, the hyostylic, or the autostylic plan.

Now, if the stages of general differentiation be indicated by points on a vertical line from which horizontal lines are drawn, and the stages of subordinate differentiation of the skull and limbs be indicated by points on a horizontal line from which vertical lines are drawn, we shall have vertical series of intersections indicating general differentiation, and horizontal series of intersections indicating special differentiation. Every known form will occupy some given intersections, and the unoccupied intersections will indicate unfulfilled, or unknown, possibilities of organization.

The Table on the following page exhibits the groups of the Ichthyopsida arranged according to this scheme.



I. HOLOCRANIA.
A. Amphiibna.
a. Pneumatocœla.
1. operculata.
2. inoperculata.
b. Apneumatocœla.
1. operculata.
2. inoperculata.
B. Monorhina.
1. operculata.
2. inoperculata.
II. ENTOMOCRANIA.
1. operculata.
2. inoperculata.
Autostylica.
Amphistylica.
Hyostylica.
AMPHIBIA (caducibranchiate).
AMPHIBIA (perennibranchiate).
Dipnoi.
CHIMÆROIDEI.
Cestracion Notidanus.
Most Selachii.
Raii.
Polypterus.
Most GANOIDEI.
TELEOSTEI.
PALÆICTHYES (Günther).
MARSIPO-BRANCHII.
PHARYNGO-BRANCHII.
Unibasal.
Tribasal.
Multibasal.
Chiropterygium.
Archipterygium.
Icthyopterygium.
Apoda.
Pedata.

IX

ON THE POSITION OF THE ANTERIOR NASAL APERTURES IN *LEPIDOSIREN.*

Proceedings of the Scientific Meetings of the Zoological Society of London, 1876 *pp.* 180, 181. (*Received January 7th*, 1876.)

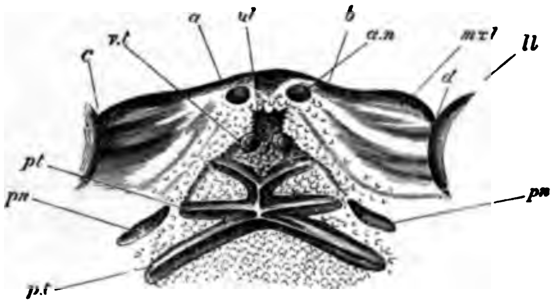
IN the course of the discussion which followed my paper on *Ceratodus*, read before the Society on the 4th of January, reference was made to the position of the anterior nasal apertures in *Lepidosiren* ; and they were affirmed to be within the mouth, inasmuch as they are situated between the upper and the lower lips.

The anterior nasal apertures correspond with the primitive openings of the olfactory sacs, which, in all known Vertebrata, are invariably developed from the integument of the under aspect of the head, in front of the region which forms the roof of the oral cavity ; and, in all the vertebrated animals in which I had specially studied the question, I had found the anterior nasal apertures to be situated in front of the upper lip and therefore outside the mouth. That they should be situated behind, or below, the upper lip, and therefore inside the mouth (so far as the cavity included between the lips may be properly called the mouth), appeared to me to be a singular anomaly, the existence of which, however, I was not prepared to dispute without re-examination of the facts. The point is, in various respects, of so much interest that I have lost no time in making the requisite investigation, with the result of leaving no doubt whatever in my mind that in *Lepidosiren*, as in *Ceratodus*, the anterior nasal apertures are truly outside the mouth, not only in the sense of lying beyond the contour of the mandible, when this is shut against the palate, but in the sense of being situated on the underside of the head in front of the upper lip, and therefore

altogether beyond the limits of any permissible definition of the oral cavity.

When the mouth of a *Lepidosiren* (*L. annectens*) is laid open from below, and the palate and the contour of what has hitherto been termed the upper lip (see fig. below, *c a b d*) are displayed, the latter is seen to present a median portion (*a b*) separated by a slight undulation from the two lateral prolongations *c a* and *b d*. The latter are the edges of the fold which overhang the mandible on each side when the parts are undisturbed. They occupy the maxillary region of the head, and may be termed the *maxillary lips*.

The median portion of the anterior contour (*a b*) does not belong to the lips at all, but corresponds, as is easily seen in a section of the skull, with the anterior extremity of the chondrocranium and the ventral edges of the nasal capsules. The line *a b* is, in fact



Under view of the fore part of the roof of the mouth and underside of the head of a young specimen of *Lepidosiren annectens* (× 3). *a b*, anterior margin of the head; *a c*, *b d*, right and left maxillary lips; *a.n*, anterior nasal apertures; *p.n*, posterior nasal apertures; *u.l*, præmaxillary lip; *v.t*, vomerine teeth; *p.t*, palatine teeth.

the anterior contour of the head; and the pigment-cells of the dorsal integument are here continued on to the ventral face. After a very short distance, however, the integument terminates in a slight, transverse, papillose ridge, which forms the anterior boundary of a shallow median depression; on each side of the hinder part of this depression is one of the vomerine teeth (*v.t*).

The anterior nares (*a.n*) lie immediately behind the anterior contour of the head; and their more prominent posterior lips lie in front of a transverse line drawn through the edge of the papillose ridge. It is obvious that the area included between the anterior contour of the head in front, the median fossa behind, and the anterior nares at the sides, corresponds with the region occupied by the naso-frontal process in the vertebrate embryo and with the homologous large, shield-shaped, naso-frontal integumentary plate in the

Rays and Dogfishes. The papillose ridge (*u.l*) is therefore the middle or premaxillary portion of the upper lip; and if this be so, it follows that the anterior nares in *Lepidosiren* are placed as in Chimæroids and Plagiostomi, on the under aspect of the head and outside the mouth.

I may add that *Lepidosiren* has two upper labial cartilages—one fibro-cartilaginous immediately behind the anterior nasal aperture, and the other behind the posterior nasal aperture. These answer to the upper labial cartilages in *Chimæra* and *Cestracion.*

X

ON THE NATURE OF THE CRANIOFACIAL APPARATUS OF *PETROMYZON*

The Journal of Anatomy and Physiology, vol. x., 1876, *pp.* 412–429.

PLATES XVII. [PLATE 6], XVIII. [PLATE 7].

IN the first part of the 'Vergleichende Anatomie der Myxinoiden published in 1835, Johannes Müller gave an exact and exhaustive account of the form and arrangement of the various parts which make up the cartilaginous skeleton of the skull and face in the Lampreys. He distinguishes a 'Hirn-capsel' or *brain case*; two 'Gehör-capseln' or *auditory capsules*; a 'Nasen-capsel' or *olfactory capsule*; and 'Gesichts-knochen' or *facial cartilages*. The latter are, in front, a 'Ringförmige knorpel-stuck' or *annular cartilage*; two 'Griffel-förmige Knochen' or *styliform cartilages*, connected by their anterior ends to the annular cartilage and by their posterior ends giving attachment to lateral muscles; a 'vordere grosse Mundschild' or *anterior dorsal cartilage*; a 'hintere Mundschild' or *posterior dorsal cartilage*; two 'vordere Seiten platten' or *antero-lateral cartilages*; and two 'zweite Seiten platten' or *postero-lateral cartilages*.

The *Brain case* consists of a *basilar plate*, the centre of which is traversed by the anterior end of the notochord. This is continued superiorly into the narrow *occipital arch*, which forms the only cartilaginous part of the roof of the skull; while laterally it passes into two cartilaginous bars, which bound the lower lateral regions of the skull. The brain rests upon a fibrous membrane stretched between these, which may be termed the *sub-cerebral membrane*. The inner and ventral edge of each of these *lateral bars* of the skull is continued into a solid cartilaginous floor, which lies between the naso-palatine canal and the mucous membrane of the mouth. Müller terms this

the *hard palate*. It terminates behind by an excavated edge between the *auditory capsules*; while, in front, it is closely united with the hinder edge of the posterior dorsal cartilage. The olfactory capsule rests on this cartilage, and is united with the lateral bars of the skull, and the naso-palatine canal extends backwards, between the subcerebral membrane and the hard palate, to terminate in a cæcal dilatation behind the posterior edge of the latter.

The anterior end of the hard palate is prolonged outwards and downwards on each side into an *anterior lateral process* ('Vorder-seiten Fortsatz'); this meets at an acute angle with a *posterior lateral process* ('Hinter-seiten Fortsatz'), which at its dorsal end is closely connected with the auditory capsule. Diverging from the dorsal or attached extremity of this, at an acute angle, is the downwardly directed *styliform process* ('Stielformige Fortsatz, *i*'). With the ventral extremity of this, the elongated horizontally directed *cornual cartilage* ('Knorpelplatte, am Fortsatz *i* befestigt; dient zur Befestigung der Zungenmuskeln') is connected.

In the middle ventral line is the long *lingual cartilage* ('knorpeliger Stiel der Zunge'), which is pointed behind, but bifurcates in front, the two short branches supporting the lobes of the tongue.

On the ventral side of this is another, elongated, but much shorter cartilage, the *median ventral cartilage* ('Zungenbein'), the anterior end of which is transversely enlarged, and lies immediately on the ventral side and in front of the anterior end of the lingual cartilage. The extremities of the anterior end of this cartilage are connected with the antero-lateral cartilages, which again are united by ligamentous fibres with the inner surface of the anterior dorsal cartilage close to its anterior edges.

Müller considers that the annular cartilages answer to the labial cartilages of the Elasmobranchs; that the styliform process and the cornual cartilages, with the median ventral cartilage, correspond with parts of the hyoidean arch in other Vertebrata; that the lateral bars of the skull are the homologues of the palatine bones of the latter; and that the inverted subocular arch formed by the anterior and posterior lateral processes corresponds with the "temporale, tympanicum, jugale, transversum, pterygoideum (?) of Cuvier" in "Osseous Fishes" (*l. c.* p. 163). He is further of opinion that the posterior dorsal cartilage has nothing to do with the skull, and that, together with the anterior dorsal cartilage and the lateral cartilages, it forms a series of structures special to the Lampreys and not represented in other Vertebrates (*l. c.* p. 164).

Agassiz, in the 'Recherches sur les Poissons fossiles' (Tome 1,

1835–43), availing himself of Müller's description and figures, and of the embryological investigations of Vogt, makes a most important rectification in the nomenclature of the parts.

In describing the skull of *Ammocœtes branchialis* (p. 113) he justly states that it corresponds with that of the embryo at the moment of the first appearance of cartilage. "The point of the notochord advances freely into the space comprised between the 'anses latérales' absolutely as in the embryo of Salmonidæ."

In *Petromyzon* he recognizes the "anses latérales" in the lateral cranial bars described by Müller and regarded by him as palatines. The subocular arch is the "*arc pterygoidien*," which, in the Cyclostomes, as in embryos, is not yet separated from the cranium by articular faces.[1] The styliform cartilage is considered to be the hyoid, while the other cartilages are reckoned as labial.

In 1844–6, Professor Owen[2] gave the following account of the structure of the lamprey's skull :—

"In the lamprey (*Petromyzon*, fig. 26) the occipital cartilage is continued backwards in the form of two slender processes (*c*) upon the under part of the chorda dorsalis (*ch*) into the cervical region. The hypophysial space (*hy*) in front of the occipital cartilage remains permanently open, but has been converted into the posterior aperture of the naso-palatine canal. The sphenoidal arches (5) are very short and approximated towards the middle line and the presphenoid and vomerine cartilage (13) is brought back closer to the sphenoidal arches. Two cartilaginous arches (24) circumscribe elliptical spaces outside the presphenoid plate : these appear to represent the pterygoid arches, but, as in the embryo of higher fishes, are not separated from the base of the skull by distinct joints. The basal cartilages after forming the ear capsules (16) extend upwards upon the sides of the cranium (fig. 11), arch over its back part, and leave only its upper and middle part membranous, as in the human embryo, when ossification of the cranium commences. Two broad cartilages (*ib.* 20, 21) may represent upon the roof of the infundibular suctorial mouth the palatine and maxillary bones, and anterior to these there is a labial cartilage (*ib.* 22). There are likewise cartilaginous processes (*ib. r. s.*) for the support of the large dentigerous tongue and the attachment of its muscles" (*l. c.* pp. 72, 3).

It appears from the context (p. 71) that by "sphenoidal arches" Professor Owen means the *trabeculæ cranii* of Rathke, as he applies

[1] l. c. p. 114. At p. 132, what is here termed "*arc pterygoidien*," is named "*arc palatin*."

[2] 'Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals,' 1846.

the term to the *anses latérales* described by Vogt in *Coregonus*, which are nothing but these *trabeculæ*, and the homology of which with the lateral bars of the cranium in the lampreys, had already been pointed out by Agassiz.

In 1858 I stated that "the skull of the lamprey is readily reducible to the same plan of structure as that which is exhibited by the tadpole, while its gills are still external and its blood colourless,[1]" having been led to that conviction by a careful study of the early stages of development of the frog's skull.

In 1863[2] I expressed this view more fully, and compared the margin of the oval space upon the base of the skull to the divergent *trabeculæ cranii*, as Agassiz had originally done, and the posterior dorsal plate to the ethmo-vomerine cartilage. I expressed the opinion that the inverted cartilaginous arch which gives attachment to the hyoidean and mandibular apparatuses of a tadpole is "strictly comparable" to the subocular arch of the lamprey; but I added a doubt "whether the accessory buccal cartilages can be strictly compared to anything in other fishes, though some of them are doubtless, as Müller has suggested, the analogues of labial cartilages.' I gave a figure (fig. 75) showing the true relation of the skeleton to the enclosed soft parts in *Petromyzon marinus*.

In his masterly monograph upon the cephalic skeleton of the Selachians,[3] Gegenbaur explains that he has taken the skull in the Selachians and not that of the more lowly organized Cyclostome for the starting-point of his investigations, because the latter are in many respects abnormal and so much less directly affiliated with the other Vertebrata, that it is not wise to attempt to begin with them. He approves of the sharp line of demarcation which Haeckel has drawn between the Lampreys and Hags, as *Monorrhina*, on the one hand, and all the higher Vertebrata, as *Amphirrhina*, on the other; and though he admits the possible correctness of the interpretation of some of the parts which I have given, he doubts whether it really tends to bridge over the hiatus.

'Da mir das Knorpelcranium der Selachier zum Ausgangspunkt so wichtig erschien, weil es einen tiefer stehenden Zustand repräsentirt, bedarf es noch der Rechtfertigung wegen des Ausschelusses der Cyclostomen, die gleichfalls mit einem Knorpelskelete versehen und zudem noch in der ganzen übrigen Organisation eine tiefere Stufe einnehmend, jenen Anförderungen noch besser hätten entsprechen

[1] Croonian Lecture, 'Proceedings of the Royal Society,' 1858.

[2] 'Lectures on the Elements of Comparative Anatomy, on the Classification of Animals, and on the Vertebrate Skull,' 1864, p. 194.

[3] 'Das Kopfskelet der Selachier,' 1872.

müssen. Darauf kann erwiedert werden, dass sowohl in dem Cranium wie in vielen Punkten ihrer übrigen Organisation die Cyclostomen bedeutend abweichende Verhältnisse darbieten und keinen so directen Anschluss an die übrigen Wirbelthiere bieten. Sie würden daher von Haeckel mit allem Recht als Monorrhina den Amphirrhinen gegenüber gestellt. Die darin ausgesprochene Auffassung kann kaum schärfer präcisirt werden. Von so abweichenden keine stricten Vergleichungen zulassenden Formen auszugehen, wäre kein glücklicher Gedanke. Wenn auch die Deutungen, welche Huxley einzelnen Theilen des Craniums gab, dasselbe dem Cranium der Amphirrhina näher gerückt scheint, so besteht darüber doch keineswegs Sicherheit. Die gewiss vorhandene Verbindung mit den Amphirrhinen mag noch zu weisen sein, aber die Entfernung, welche zwischen diesen und den Cyclostomen liegt, wird dadurch nicht vermindert.'[1]

In describing the skull of *Menobranchus lateralis*,[2] I have remarked that

"No known Elasmobranch, Ganoid, or Teleostean fish presents so incompletely developed a chondrocranium as that of *Menobranchus*. On the other hand, the latter is much like that of a Lamprey if we leave the ossification of the *Menobranchus* skull and the accessory cartilages of the *Petromyzon* out of consideration. And this fact, taken together with the curious resemblance in development between the Lampreys and the Amphibia (which are much closer than those between any of the higher Fishes and the Amphibia[3]) suggest to my mind the supposition that, in the series of modifications by which the Marsipobranch type has been converted into that of the higher fishes, the most important terms must have been forms intermediate in character between the *Dipnoi* and the Marsipobranchii" (*l. c.* pp. 197, 8[4]).

Finally, in a 'Preliminary Note upon the Brain and Skull of *Amphioxus lanceolatus*,' read before the Royal Society last year, I compared the skull of the Lamprey in its *Ammocœtes* stage with that of *Amphioxus*, with the view of showing (1) that numerous

[1] Gegenbaur, 'Das Kopfskelet der Selachier,' Einleitung, p. 9, 1872.

[2] 'Proceedings of the Zoological Society of London,' 1874.

[3] Unfortunately we know nothing of the development of the *Dipnoi*.

[4] I have not yet had time to study Goette's large and elaborate work on the development of Bombinator igneus ('Entwickelungsgeschichte der Unke,') published this year, with the attention it deserves; but I notice at p. 692, the remark, that "der vollendete Zustand des Kopfes, wenigstens der Neunaugen ganz entschieden auf die Anuren-larven hinweist." I am further glad to find that Dr. Goette takes the same view as I have done respecting the relations of the *Anura* with the Cyclostomes (p. 744).

anterior proto-vertebræ, answering to those which in the higher Vertebrata give rise to vertebræ (among other products of their metamorphosis), but which neither in the head, nor in any other part of the body of *Amphioxus* develop vertebræ, correspond with the region in which the chondrocranium is developed in the Ammocœte, and (2) that neither in the Ammocœte do these proto-vertebræ give rise to vertebræ, but that the brain-case, as in *Menobranchus*, is formed partly by the parachordal cartilages (which are chondrifications of the investing mass of the notochord, comparable to that which precedes the development of the vertebræ in the spinal column of the Frog); and partly by the trabeculæ which in my view, are homologous with branchial arches.[1] In the Croonian Lecture to which I have already referred, the following passage occurs :—

" The cranium never becomes segmented into somatomes : distinct centra and intercentra like those of the spinal column are never developed in it. Much of the basis cranii lies beyond the notochord. In the process of ossification there is a certain analogy between the spinal column and the cranium, but that analogy becomes weaker and weaker as we proceed towards the anterior end of the skull.

" Thus it may be right to say that there is a primitive identity of structure between the spinal or vertebral column and the skull ; but it is no more true that the adult skull is a modified vertebral column, than it would be to affirm that the vertebral column is a modified skull."

The immense extension of our knowledge of the minute details of the structure and development of the vertebrate skull in the seventeen

[1] Goette has put forward a very different view of the nature of the trabeculæ (*l. c.* p. 629). "The original foundation of the whole skull consists firstly, of the posterior basis cranii, a cartilaginous plate, which incloses the notochord, in which I distinguish, as in the trunk, an axial part, the notochord with its external sheath, and lateral plates homologous with the arches of the vertebræ." (This answers to what I have named the parachordal portion of the skull.) "To this are added the two pair of arches, which, as continuations of these lateral plates, at their anterior and posterior ends, embrace laterally, and eventually arch over the anatomical base of the fore-brain and a part of the hind-brain. This anterior pair of arches belongs therefore to the first segment of the body under discussion ; it forms the first vertebral arch, which in agreement with the general position of this segment is horizontal. But it has no corresponding centrum—inasmuch as the axial structure by which the latter should be produced, the notochord, was drawn back from the fore-head (Vorderkopf) to the anterior margin of the hind-head." According to this interpretation, which is worthy of serious consideration, though I entertain grave doubts whether it can be sustained, the trabeculæ represent not the most anterior pair of visceral arches, as I have supposed, but the most anterior pair of neural arches. How this view is to be reconciled with the relations of the trabeculæ to the trigeminal nerve and to the organs of the higher senses, is not clear to me.

years that have elapsed since those words were written, and which is largely due to the investigations of Mr. Parker, whose elaborate and numerous contributions to this difficult branch of anatomy seem hardly to be as well known as they ought to be abroad,[1] has, so far as I know, revealed no fact inconsistent with their fullest signification.

The segments of the *Amphioxus* head are not vertebræ, and in the Lamprey, as in every known vertebrate animal, the cranial region takes on the characters of a skull without passing through any stage of vertebration.[2]

At the end of my brief paper I stated that I proposed at some future time to show "in what manner the skull of the Marsipobranch is related to that of the higher vertebrata, and more especially to the skull of the frog in its young tadpole state."

For this purpose it was needful to go over the structure of the lamprey's skull afresh, and unfortunately my supply of these fish was small, and I have been unable to procure fresh ones until recently. I have examined them by the ordinary way of dissection, and by making transverse sections which form admirable Canada-balsam preparations.

The dorsal wall of the circular lip which surrounds the mouth of the lamprey (Plate XVII. [Plate 6] Fig. 1) is longer than the ventral wall, and hence has the form of a hemispherical bell, set obliquely on to the body. On the ventral side, the lip is separated by a deep transverse constriction from the rest of the head, but this constriction dies away laterally, and hardly any trace of it remains on the dorsal aspect. The inner surface of the lip is beset with the well-known horny teeth, and its margins are provided with numerous short lamellar papillæ, of which those on the ventral side are the longest and largest.

The opening into the buccal chamber, in the posterior and dorsal region of the bell-shaped cavity of the lip, is small. Immediately below it is a projection (Plate XVII. [Plate 6] Fig. 1, *o*) convex forwards, flat or concave on its dorsal aspect, and having a horny envelope, the edge of which is produced into a number of denticulations, the longest of which is median. I shall term this the *mandibular*

[1] For example, I do not find Mr. Parker's name in the long "Autoren Verzeichniss" appended to Goette's work, though the memoir 'On the Structure and Development of the Skull of the Common Frog,' the best piece of work of its kind which has appeared since Dugès' 'Recherches,' was published in 1871.

[2] It is to be hoped that this statement will prevent persons of even the largest powers o. misunderstanding from imagining that the demonstration of the multi-segmentation of the head of *Amphioxus*, is a relapse on my part into archetypal fancies such as those of which I endeavoured to show the futility a score of years ago.

tooth. On the ventral side of it is a transverse fold which bears two papillary eminences. The *annular cartilage* (*a*) is lodged in the posterior part of the lip, and its ventral part lies just below this fold.

The *inferior median cartilage* (Plate XVII. [Plate 6] Fig. 1, *l*) lies beneath the integument, and separated from it by a large subcutaneous sinus,[1] amidst the ventral muscles. The anterior edge of the crosspiece in which it terminates is connected by fibrous tissue with the support of the mandibular tooth. Behind the latter, the tongue (*p*) rises from the floor of the buccal cavity and nearly closes it. It is divided by a deep longitudinal groove into two lobes, united for a short distance in front. The opposed surfaces of these lobes, present minute horny denticulations arranged in a curved anteroposterior series.

The *buccal cavity* itself has the form of an elongated tube with delicate and transparent walls. Its roof is folded longitudinally so as to form a groove (Plate XVIII. [Plate 7] Fig. 1, *g*) which is much deeper in front than behind. A small papillose elevation (*t*) bounds the anterior end of this groove, and for a short distance from its commencement its sidewalls are obliquely folded. This buccal portion of the alimentary canal terminates behind by dividing into two tubes, one of which lies on the dorsal side of the other, both occupying the median plane. The upper tube (Plate XVII. [Plate 6] Fig. 1, *œ*) is the very slender *œsophagus* which traverses the whole length of the branchial region to pass into the gastrointestinal division of the alimentary canal. The lower, much larger tube is the so-called 'respiratory bronchus,' or *branchial canal* (*Br*). The wall of the buccal cavity between these two tubes is produced into a sort of horizontal shelf, the free edge of which is directed forwards and is divided into five tentacular processes, of which the median is the shortest (Plate XVII. [Plate 6] Fig. 1, *f*; Plate XVIII. [Plate 7] Fig. 1, *u*). These overhang the entrance of the branchial canal, and doubtless serve to prevent the entrance of solid particles into it. Two small flat pieces of cartilage which are wide in front and narrow behind, and are similar in colour to the other cartilages, support the horizontal shelf from which the tentacles spring. They diverge outwards and backwards towards the styliform processes. The axis of each tentacle and the middle of the 'shelf' between the two cartilages just described, are occupied by a colourless cartilaginous tissue. Behind and below this

[1] This communicates with the system of cavities described as Lymphatic by Langerhans. It contained blood in the specimens I examined. See Milne-Edwards' 'Leçons,' III. p. 69.

tentaculated shelf the entrance of the branchial canal is further protected by two folds of the lining membrane (Plate XVII. [Plate 6] Fig. 1, *r*; Plate XVIII. [Plate 7] Fig. 1, *vl*), the free edges of which are directed backwards and towards one another. The dorsal half of each of these valves is nearly vertical; the ventral half slopes backwards until it becomes nearly horizontal. These valvular folds constitute the *pharyngeal velum*, and are, doubtless, the metamorphosed velum of the Ammocœte. They must readily allow of the passage of water into the branchial canal, but must obstruct its exit.[1] Behind these, is another smaller and much more delicate pair of valvular folds (Plate XVIII. [Plate 7] Fig. 1, vl^2) which when they flap back, cover the first internal branchial aperture. There is a depression behind each of the pharyngeal vela, and a bristle could sometimes be passed through the wall into a small space outside it. This I conceive to be the remains of the hyoidean cleft which opens externally in the Ammocœte.[2]

When the lining wall of the buccal cavity is removed, two large muscles are seen to lie between it and the lateral skeletal parts. The upper is attached by a long tendon to the middle of the hinder edge of the anterior dorsal cartilage, on each side of the papillose elevation at the anterior end of the dorsal groove already described. The lower, fleshy throughout its length, is inserted into the tongue. Each of these muscles arises from the styliform process, the position of which exactly corresponds with that of the outer attached edge of the velum. Immediately subjacent to the ventral wall of the buccal cavity lies the strong aponeurotic sheath of the lingual muscles with the lingual cartilage (Plate XVII. [Plate 6] Fig. 1, *k*), which they ensheath. The two *cornual cartilages* (*i*) are imbedded in this sheath, their long edges being close to, and nearly parallel with, one another (Plate XVIII. [Plate 7] Fig. 3).

Thus it is obvious that the *lingual cartilage* has the same relations as the median ventral element of the hyoidean arch in the higher Vertebrata, and that the *cornual cartilages* and the *styliform processes* represent lateral elements of the same arch. Müller attached the same signification to the cornual cartilages, but not to the lingual cartilage.

In this case what is the *median ventral cartilage* which Müller regarded as the body of the hyoid? The hyoidean arch is complete without it and has no special connection with it, the bent up anterior end of the lingual cartilage simply playing over it. I conceive it to

[1] See Stannius, 'Handbuch der Zootomie,' I. p. 240, and Rathke's description of these parts in his 'Bemerkungen ueber den innern Bau der Pricke,' 1825.

[2] 'Proceedings of the Royal Society,' 1875, p. 128, Fig. D. 1.

be a median ventral element of the mandibular arch ; notwithstanding that, in the higher vertebrates, such an element, though the analogy of the other arches would lead us to expect its presence, is not known to occur.

The third division of the trigeminal nerve passes over the expanded anterior end of this cartilage, traverses the ventral half of the annular cartilage, and runs along the anterior edge of the latter to its dorsal extremity.[1] Thus although its halves are united dorsally, the annular cartilage would seem to be essentially a post-oral structure. The inverted subocular arch formed by the posterior (*f*) and anterior (*f'*) lateral processes lies at the sides of the posterior part of the buccal cavity. The second and third divisions of the trigeminal nerve (Plate XVIII. [Plate 7] Fig. 1, V^2, V^3) perforate the membrane which connects them, the third running obliquely downwards and forwards to its distribution (Plate XVII. [Plate 6] Fig. 1); the second turning outwards and passing to the sides of the head.

The posterior lateral process therefore answers, in all essential respects, to the suspensorial cartilage or proximal division of the mandibular arch, though possibly the dorsal end of the hyoidean arch may be united with it.

Having proceeded thus far, the further study of the craniofacia apparatus of the Lampreys will be facilitated by comparison with that of the tadpole (of *Rana temporaria*) in the stage in which the right opercular cleft is closed, while the hind-limbs are still in the condition of mere buds (Plate XVII. [Plate 6] Fig. 2 ; Plate XVIII. [Plate 7] Figs. 2, 4 and 6).

Dugès has given an admirably clear and accurate account of the structure of the skulls of the tadpoles of *Pelobates fuscus*, *Hyla viridis*, and *Rana esculenta* in this stage ; and it has subsequently been treated of by Reichert, by myself and by Mr. Parker (*Phil. Trans.*, 1871). Figures of a somewhat more advanced condition of the skull of *Bombinator igneus* are given by Goette in the work already cited.

The skull of the tadpole, at this stage, consists of a cartilaginous parachordal basilar plate, the middle of which contains the anterior end of the notochord. On each side are the auditory capsules, while, in front, the basi lar plate extends forwards on each side of the pituitary space to form the trabeculæ. These unite in front, but speedily diverge again to terminate abruptly, close to the upper labial cartilages (Plate XVIII. [Plate 7] Fig. 2, *U. lb*). The nasal sacs are

[1] See Born, 'Ueber den inneren Bau der Lamprete,' Heusinger's 'Zeitschrift,' 1827, Tab. VI. fig. 7.

situated on the dorsal aspect of the head, one on each side of the origin of these ethmoidal processes of the skull (*e*), and they open directly into the anterior part of the buccal cavity. On comparing this skull with that of the young Ammocœte (Plate XVIII. [Plate 7] Fig. 5) the justice of the comparison instituted by Agassiz, between the 'anses' of the latter (*Tr*) and the trabeculæ of vertebrate embryos in general becomes manifest. Only, in the Ammocœte, there is, as yet, nothing answering to the ethmoidal processes of the Frog's skull.

In the young Ammocœte again the median nasal sac (*Na*) is conical and its brief ventral prolongation merely overlies the commissure of the trabeculæ. If the sac could be divided into two by a median constriction it would answer to the nasal sacs of the Frog before they communicate with the buccal cavity. The only representative of any part of the subocular arch of the adult, in the Ammocœte stage of the Lamprey, is a slender cartilaginous process (*g*) which corresponds with the dorsal end of the posterior lateral process of the adult.[1]

It is obvious from the position of the lateral bars of the cranium in the Lamprey that they are, as Agassiz determined them to be, homologous with the 'anses' of the Ammocœte and therefore are modified trabeculæ—while the 'hard palate' is a chondrification of the tissue which lies between them, corresponding with that process of chondrification by which the floor of the skull in the Frog becomes completely converted into cartilage.

Nor in my judgment, can it be doubted that the posterior dorsal cartilage of the Lamprey answers to the ethmoidal processes of the tadpole's skull, the interspace between them being similarly chondrified.

Again, at the sides of the Frog's skull there is a subocular arch (Plate XVIII. [Plate 7] Fig. 2, *p*, *f*, *g*), the posterior limb of which (*g*) is in all respects comparable to the corresponding part of the Lamprey's subocular arch; except so far as the styliform cartilage of the Lamprey may possibly represent the upper end of the hyoidean arch. For in the Frog, as I pointed out in my paper on *Menobranchus*, the hyoidean arch is simply articulated with the suspensorium and does not coalesce with it.

I have formerly assumed that the anterior pillar of the subocular arch in the tadpole (Plate XVII. [Plate 6] Fig. 2; Plate XVIII. [Plate 7]

[1] When this passage was written I had not seen the valuable paper of Langerhans, 'Untersuchungen über Petromyzon Planeri,' Freiburg, 1873. I find that he has described and figured the process here mentioned, as well as the cartilaginous olfactory capsule known to Rathke, but overlooked by Müller.

Fig. 2, *p*.) answers to the anterior lateral process in the Lamprey, to which it is indeed extraordinarily similar. But further consideration shows that there is a difficulty in the identification of the two. Both the second and the third divisions of the trigeminal nerve pass through the subocular membrane, and therefore on the ventral side of the arch; whereas in the Frog, as in all other Vertebrata, they run on the dorsal aspect of the palatine arcade. This is a singular anomaly (which occurs also in the Myxinoids), and it leads to the suspicion that the anterior lateral process may be represented, not by the palatine process of the suspensorium of the tadpole (*p*, Fig. 2), but by the orbital process, which, as is well known, arches over the jaw-muscles and nerves until it reaches the skull, with which it becomes united by fibrous tissue.

The otic process of the tadpole's suspensorium has no representative in the Lamprey, and therefore the posterior division of the seventh nerve, which takes the same course as in the Frog, does not pass through a foramen.

The oral aperture of the tadpole, in this stage, is surrounded by a deep, fringe-like, transversely-oval lip, produced on each side into a fold (Plate XVIII. [Plate 7] Fig. 6). Dorsally, this lip, as in the Lamprey, passes evenly into the integument of the head; ventrally, it is marked off from the rest of the integument, just as in the Lamprey, by a deep transverse constriction. The inner surface of the lip is raised into ridge-like linear elevations, the free edges of which are beset with the singular spoon-shaped serrated hooks, which result from the modification of the epithelium.

There are four rows of these denticles in the lower division of the lip, and two in the upper. Behind these come the horny jaws, which are structures of a very similar nature, moulded upon the edges of two pairs of labial cartilages—an upper and a lower (*U. l b*; *L, l b*).

Each pair of these labial cartilages are so closely united in the middle line in this stage that it is not always easy to discern the traces of their primitive distinctness. The upper pair overlap the lower, which last form a half circle. In *Rana temporaria* the second small upper labial cartilage attached to the outer angle of each of the principal pair, which is described and figured by Dugès in *Pelobates*, appears to be absent.

The angles of the upper and lower labial cartilages are united by fibrous tissue. The outer part of the dorsal face of each lower labial cartilage articulates with the outer end of the posterior face of the short Meckelian cartilages (*Mk*). These are therefore separated by a considerable interval, occupied by the floor of the mouth (Plate XVIII.

[Plate 7] Fig. 4). Their proximal ends articulate with the ends of the suspensoria, and the long axis of each Meckelian cartilage is inclined downwards and backwards. These cartilages therefore lie at the sides of, as well as beneath the buccal cavity (Plate XVII. [Plate 6] Fig. 2).

The larger hyoidean cornu (Plate XVIII. [Plate 7] Fig. 4, Hy^1), articulated with the posterior face of the suspensorium by a part of its anterior edge, ends dorsally in a free point; ventrally, it narrows and passes into the anterior, transversely expanded, end of a median cartilage (Hy^1), which tapers posteriorly, and is received between the coalesced ventral ends of the branchial arches. Of these there are four. The ventral part of the most anterior is still distinctly marked off from the coalesced ventral ends of the three posterior arches. The dorsal moieties of the branchial arches, when they are separated by the branchial clefts, are bent so as to be strongly convex outwards and concave inwards.

The cornu of the hyoid in the tadpole obviously answers to the *cornual cartilages* in the Lamprey. The median cartilage, the anterior expanded end of which raises the mucous membrane of the anterior part of the floor of the mouth into a rudimentary tongue, no less closely resembles the *lingual cartilage* of *Pteromyzon*, while the branchial arches represent the four anterior branchial arches of the Lamprey. Not only so, but in the present stage the branchiæ of the tadpole are, as is well known, pouches, which present no merely superficial likeness to the branchial sacs of the Lamprey. A septum extends inwards from the concave face of each branchial arch, and the septa of the two middle arches (Plate XVIII. [Plate 7] Fig. 4) terminate in free edges in the branchial dilatation of the pharynx. Vascular branchial tufts beset the whole convex outer edge of the branchial arch, and are continued inwards in parallel transverse series of elevations, which become smaller and smaller towards the free edge of each septum, near which they cease.[1]

In the young Ammocœte the septa of the branchial chambers similarly bear vascular processes, which are first developed close to the external branchial aperture, and thence extend inwards transversely.[2]

The recesses at the sides of the floor of the pharynx into

[1] Dugès (*l. c.* p. 97) has carefully described the branchiæ of *Pelobates*.

[2] If these first-formed long branchial filaments of the Ammocœte projected through the small gill-clefts outwards instead of inwards, they would resemble the first-formed "external gills" of Elasmobranchs. And this difference of direction seems to indicate the solution of the difficulty, that external gills, which are so generally developed at first in *Elasmobranchii*, *Ganoidei* and *Dipnoi*, are apparently wanting in *Marsipobranchii*.

which the interceptal clefts, or internal branchial clefts open, answer, taken together, to the branchial canal of the Lamprey, which is not shut off from the œsophagus in the Ammocœte. The anterior boundary of each of these recesses is marked by a fold of the mucous membrane, the free edge of which projects backwards and is produced into papilliform angulations so as to appear scalloped (Plate XVIII. [Plate 7] Fig. 4). The anterior face of this fold is convex, its posterior face is concave. The inner angle of each fold passes into its fellow by a ridge, produced into one or two papillæ, which is closely adherent to the median part of the floor of the mouth. The outer angle is continued into a more delicate fold of the mucous membrane lining the roof of the mouth, the free edge of which also projects backwards. It is plain that these structures answer to the pharyngeal velum of the Lamprey.[1]

Thus I think there can be no doubt that the cornua of the hyoid in the Frog, and the median cartilage which connects them, are the homologues of the cornual cartilages and the lingual cartilage of the Lamprey. Whether the styliform process of the Lamprey is really the upper end of the hyoidean arch, or whether it simply answers to the part of the mandibular arch of the tadpole which articulates with the hyoidean cornu elongated into a process, is more than I can, at present, venture to decide. The analogy of the frog and of *Chimæra* however is against the hyoidean nature of the styliform process. The lower labial cartilages in the tadpole (*l.lb*) occupy just the same position in the lip, in front of the ventral constriction, as the ventral half of the annular cartilage does in the Lamprey. Considering that the corresponding structure in *Amphioxus* is an incomplete ring open on the dorsal median line; and considering, further, the distribution of the third division of the trigeminal nerve, I incline to think that the annular cartilage of the Lamprey represents only the lower labial cartilages of the Frog. A knowledge of the development of the ring in question would decide this point, but I have not yet been able to obtain young Lampreys in which the

[1] Some very singular tentacular structures are arranged in definite order in the roo. and on the floor of the tadpole's mouth. Three or four are situated in a transverse row upon the rudimentary tongue: two over the junction of Meckel's cartilage with the lower labial cartilage: one large one immediately behind the inner or posterior nostril. Between these the roof of the mouth presents a triangular papillose elevation with its apex directed backwards—which is comparable to the papilla at the anterior end of the dorsal buccal groove in *Petromyzon*—and two parallel rows, one on each side of the roof, and one on each side of the floor of the mouth. The extremities, and sometimes the sides of these tentacula, are more or less papillose, and the central axis is in structure very similar to developing cartilage.

buccal cartilages are just making their appearance. If the annular cartilage of the Lamprey answers to the lower labial cartilages of the Frog, then the upper labial cartilages will correspond in form and position to the anterior dorsal cartilage, and the small antero-lateral cartilages will perhaps have a parallel in the upper 'adrostral' cartilages in *Pelobates.*

The *posterior lateral cartilages* are directly connected with that end of the suborbital arch which answers to the articular end of the suspensorium in the Frog (Plates XVII. [Plate 6], XVIII. [Plate 7] (figs. 1 and 2), and, in this position, exaggerate the peculiar arrangement of the tadpole's Meckelian cartilage. That they are parts of the mandibular arch I believe to be certain, but in the absence of any knowledge of their mode of development I leave the question as to their exact homology open. Finally, the median ventral cartilage appears to have no representative in the tadpole; and, as I have already said, I take it to be an inferior median piece of the mandibular arch—not represented, so far as our present knowledge goes, in the higher vertebrata.

Thus the the craniofacial apparatus of the Lamprey can be reduced to the same type as that of the higher Vertebrata, by means of the intermediate terms afforded by the Tadpole's skull; and there appears to me to be no sufficient foundation, in the present state of knowledge, for regarding the Marsipobranch skull as one which departs in any important respect from the general vertebrate type.

To what extent all the identifications here made will stand the test of the study of the development of the Lamprey's facial cartilages remains to be seen; but the only doubt which exists in my mind is with regard to the anterior dorsal and the postero-lateral cartilages. If the annular cartilage is developed by the confluence of primitively distinct upper and lower labial cartilages, the homologues of the anterior dorsal cartilage will have to be sought in some of the anomalous palatal cartilages of the Rays; among which it might not be impossible to find representatives of the postero-lateral cartilages. But that the parts of the face of the Lamprey present no structures, which are not to be found in one shape or another among the higher Vertebrata, appears to me to be clear.

In the Myxinoid *Marsipobranchii* there is even less difficulty in reducing the skull to the ordinary vertebrate type. Three pairs of cartilaginous rods here spring from the anterior end of the parachordal region, one pair passing forwards as the trabeculæ, and two curving backwards and to the ventral side as the mandibular and

[PLATE 6.]

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Fig. 1.

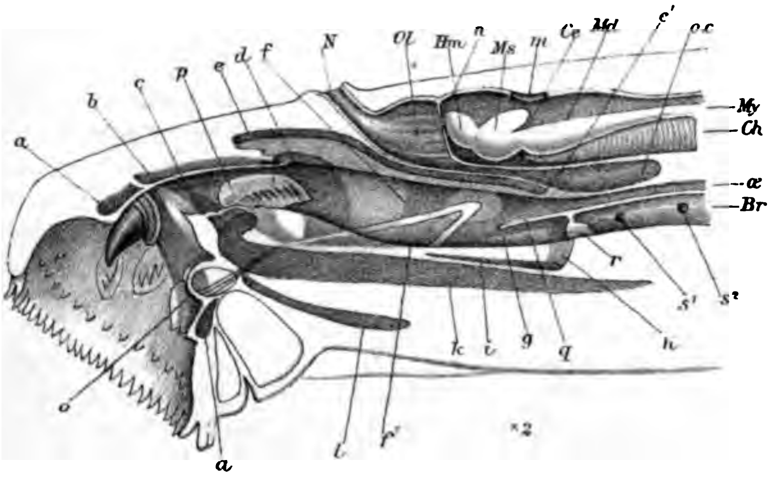
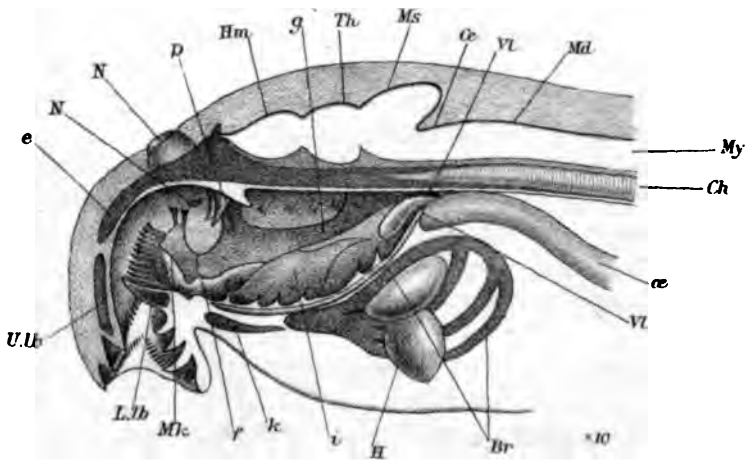


Fig. 2.



A Hammond, lith.

T. Way. Imp.

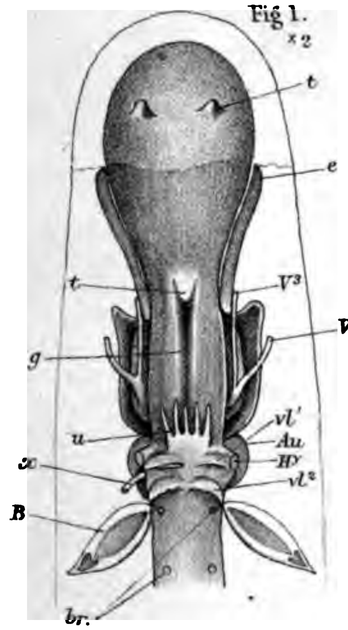


Fig. 1. ×2

Fig. 6. ×10

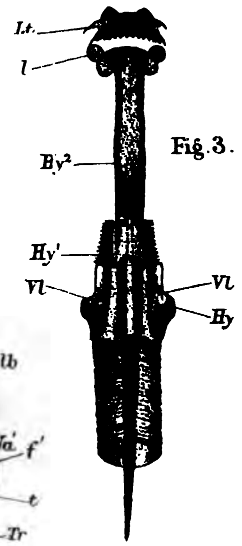


Fig. 3.

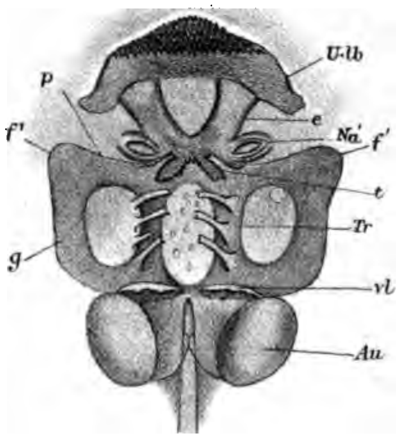


Fig. 2. ×6

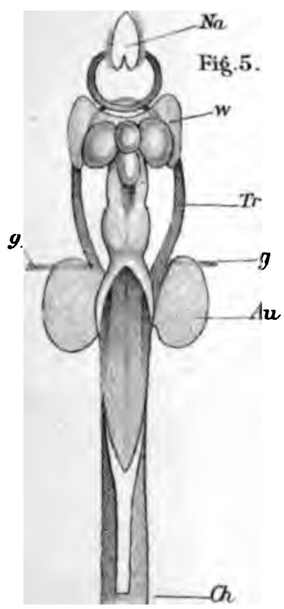


Fig. 5.

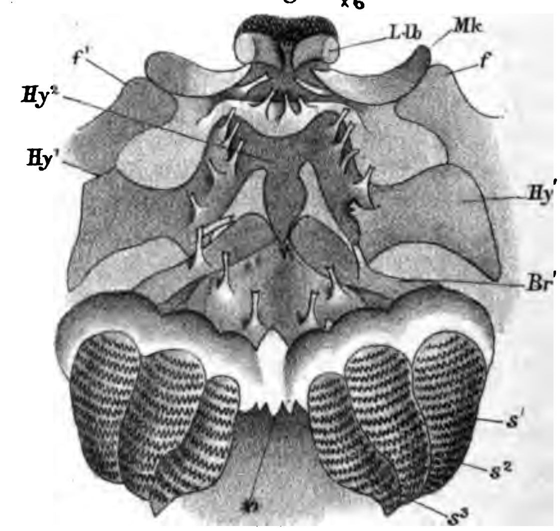


Fig. 4. ×6

A. Hammond, lith.

T. Way. Imp.

hyoidean arches respectively. The two latter have swung backwards until they take a position unlike that which they have in the Tadpole and the Lamprey, and like that which they have in the adult Frog. Not only in this respect, but in the structure of the circulatory and respiratory apparatuses the Myxinoid fishes exhibit a higher stage of organization than the Lampreys. But, at present, I can only indicate the outlines of a comparison which requires fuller discussion than can be given to it on the present occasion.

In conclusion, I will only advert to the singular resemblance in structure and mode of working between the tongue of the Marsipobranch and the odontophore of a Mollusk, as a point worthy of attention.

DESCRIPTION OF THE PLATES.

PLATE XVII. [PLATE 6]

Fig. 1. Vertical and longitudinal section of the anterior part of the body of Lamprey (*P. fluviatilis*) × 3. *a.* annular cartilage; *b.* anterior dorsal cartilage; *c.* antero-lateral; *d.* postero-lateral cartilage; *e.* posterior dorsal cartilage; *e′.* hinder margin of the hard palate; *f.* anterior lateral process; *g.* posterior lateral process; *j′.* angle formed by the junction of these; *h.* styliform process; *i.* cornual cartilage; *k.* lingual cartilage; *l.* median ventral cartilage; *m.* occipital arch; *n.* posterior wall of the nasal capsule; *o.* lip-like fold with two papillæ; *p.* tongue; *q.* tentaculate branchial valve; *r.* pharyngeal velum. *N.* nasal aperture; *Ol.* olfactory sac; *Hm.* the cerebral hemispheres; *M.* midbrain; *Ce.* cerebellum; *Md.* medulla oblongata; *My.* myelon; *Ch.* notochord; *Oc.* nasal canal.

Fig. 2. Vertical and longitudinal section of the anterior part of the body of a Tadpole of *Rana temporaria* (× 10) *Ch, My, Md, Ce., Ms., Hm., a., N. as before;* *N′.* posterior nasal aperture; *Mk.* Meckel's cartilage; *U. lb, L. lb.* upper and lower labial cartilages; *e.* ethmoidal cartilage; *f* angle of junction of the palatine cartilage, *p.* with the suspensorium, *g.* and the articular surface for Meckel's cartilage; *k.* median cartilage connecting the hyoid and branchial arches; *Br. V. V.* pharyngeal velum; *H.* heart.

PLATE XVIII. [PLATE 7]

Fig. 1. The anterior part of the roof of the branchial canal and of the buccal cavity of a Lamprey (× 3); *b.* The two anterior branchial openings; B. The right anterior branchial sac; *x.* a bristle passed into the opening behind the right half of the *velum vl.*; *vl²*. the second valvular fold in front of the first branchial aperture, more distinctly shewn than in nature; *u.* the 'shelf' with its tentacles; *g.* the median groove; *t.* its anterior termination; *e.* the anterior end of the posterior dorsal cartilage; v^2v^3. the second and third divisions of the trigeminal nerve; *Au.* the auditory capsules.

Fig. 2. The roof of the mouth of a Tadpole of *R. temporaria* (× 10) *Ch., Au.* as before--*vl.* the superior vela; *t.* a median large triangular papilla, between the two which lie behind the posterior nares; *Tr.* trabeculæ; *g. f. p.* the sub-ocular arch: *e.* the ethmoidal processes; *U. lb.* the upper labial cartilage.

Fig. 3. The lingual cartilage *Hy²*, the cornual cartilages *Hy′* and the styliform processes *Hy* (?) of a Lamprey magnified three times; *Lt.* the mandibular tooth; *l.* the anterior end of the median ventral cartilage, the posterior prolongation of which is supposed

to be seen through the lingual cartilage; *Vl.* the lower halves of the pharyngeal vela—between which a small portion of the mucous membrane of the floor of the mouth is seen. Beneath this is the fibrous aponeurosis of the muscular sheath of the tongue and the tendon of the long retractor muscle.

Fig. 4. The floor of the mouth of the Tadpole of *Rana temporaria; Llb.* lower labial cartilage; *Mk.* Meckel's cartilage; *Hy'.* hyoidean cornu; Hy^2. median inferior piece of the hyoid; *Vl.* inferior velum; *s.* 1. 2. 3. 4. walls of the branchial sacs.

Fig. 5. The skull of a young Ammocœte, or larval Petromyzon, with the brain in situ; *Ch.* the notochord; *Au.* the auditory capsules; *g.* the lateral process; *Tr.* the trabeculæ; *w.* the lateral walls of the cranium in the region of the cerebral hemispheres; *Na.* the nasal opening embraced by the crescentic cartilage.

Fig. 6. Lips and horny upper jaw of the Tadpole (× 10).

XI

ON THE BORDER TERRITORY BETWEEN THE ANIMAL AND THE VEGETABLE KINGDOMS.

Macmillan's Magazine, vol. xxxiii., pp. 373–384. (*Delivered at the Royal Institution of Great Britain, Friday, January 28th,* 1876.)

IN the whole history of science there is nothing more remarkable than the rapidity of the growth of biological knowledge within the last half-century, and the extent of the modification which has thereby been effected in some of the fundamental conceptions of the naturalist.

In the second edition of the *Règne Animal*, published in 1828, Cuvier devotes a special section to the "Division of Organized Beings into Animals and Vegetables," in which the question is treated with that comprehensiveness of knowledge and clear critical judgment which characterise his writings, and justify us in regarding them as representative expressions of the most extensive, if not the profoundest, knowledge of his time. He tells us that living beings have been sub-divided from the earliest times into *animated beings*, which possess sense and motion, and *inanimated beings*, which are devoid of these functions, and simply vegetate.

Although the roots of plants direct themselves towards moisture, and their leaves towards air and light; although the parts of some plants exhibit oscillating movements without any perceptible cause, and the leaves of others retract when touched, yet none of these movements justify the ascription to plants of perception or of will.

From the mobility of animals, Cuvier, with his characteristic partiality for teleological reasoning, deduces the necessity of the existence in them of an alimentary cavity or reservoir of food, whence their nutrition may be drawn by the vessels, which are a sort of internal roots; and in the presence of this alimentary cavity he naturally sees

the primary and the most important distinction between animals and plants.

Following out his teleological argument, Cuvier remarks that the organization of this cavity and its appurtenances must needs vary according to the nature of the aliment, and the operations which it has to undergo, before it can be converted into substances fitted for absorption; while the atmosphere and the earth supply plants with juices ready prepared, and which can be absorbed immediately.

As the animal body required to be independent of heat and of the atmosphere, there were no means by which the motion of its fluids could be produced by internal causes. Hence arose the second great distinctive character of animals, or the circulatory system, which is less important than the digestive, since it was unnecessary, and therefore is absent, in the more simple animals.

Animals further needed muscles for locomotion and nerves for sensibility. Hence, says Cuvier, it was necessary that the chemical composition of the animal body should be more complicated than that of the plant; and it is so, inasmuch as an additional substance, nitrogen, enters into it as an essential element, while in plants nitrogen is only accidentally joined with the three other fundamental constituents of organic beings—carbon, hydrogen, and oxygen. Indeed, he afterwards affirms that nitrogen is peculiar to animals; and herein he places the third distinction between the animal and the plant.

The soil and the atmosphere supply plants with water, composed of hydrogen and oxygen; air, consisting of nitrogen and oxygen; and carbonic acid, containing carbon and oxygen. They retain the hydrogen and the carbon, exhale the superfluous oxygen, and absorb little or no nitrogen. The essential character of vegetable life is the exhalation of oxygen, which is effected through the agency of light.

Animals, on the contrary, derive their nourishment either directly or indirectly from plants. They get rid of the superfluous hydrogen and carbon, and accumulate nitrogen.

The relations of plants and animals to the atmosphere are therefore inverse. The plant withdraws water and carbonic acid from the atmosphere, the animal contributes both to it. Respiration—that is, the absorption of oxygen and the exhalation of carbonic acid—is the specially animal function of animals, and constitutes their fourth distinctive character.

Thus wrote Cuvier in 1828. But in the fourth and fifth decades of this century, the greatest and most rapid revolution which biological

science has ever undergone was effected by the application of the modern microscope to the investigation of organic structure; by the introduction of exact and easily manageable methods of conducting the chemical analysis of organic compounds; and finally, by the employment of instruments of precision for the measurement of the physical forces which are at work in the living economy.

That the semi-fluid contents (which we now term protoplasm) of the cells of certain plants, such as the *Charæ*, are in constant and regular motion, was made out by Bonaventura Corti a century ago: but the fact, important as it was, fell into oblivion, and had to be rediscovered by Treviranus in 1807. Robert Brown noted the more complex motions of the protoplasm in the cells of *Tradescantia* in 1831; and now such movements of the living substance of plants are well known to be some of the most widely-prevalent phenomena of vegetable life.

Agardh, and other of the botanists of Cuvier's generation, who occupied themselves with the lower plants, had observed that, under particular circumstances, the contents of the cells of certain water-weeds were set free and moved about with considerable velocity, and with all the appearances of spontaneity, as locomotive bodies, which from their similarity to animals of simple organization were called "zoospores."

Even as late as 1845, however, a botanist of Schleiden's eminence deals very sceptically with these statements; and his scepticism was the more justified, since Ehrenberg, in his elaborate and comprehensive work on the *Infusoria*, had declared the greater number of what are now recognised as locomotive plants to be animals.

At the present day, innumerable plants and free plant cells are known to pass the whole or part of their lives in an actively locomotive condition, in no wise distinguishable from that of one of the simpler animals; and, while in this condition, their movements are, to all appearance, as spontaneous—as much the product of volition—as those of such animals.

Hence the teleological argument for Cuvier's first diagnostic character—the presence in animals of an alimentary cavity, or internal pocket, in which they can carry about their nutriment, has broken down—so far, at least, as his mode of stating it goes. And with the advance of microscopic anatomy the universality of the fact itself among animals has ceased to be predicable. Many animals of even complex structure, which live parasitically within others, are wholly devoid of an alimentary cavity. Their food is provided for them, not only ready cooked but ready digested, and the alimentary canal,

become superfluous, has disappeared. Again, the males of most Rotifers have no digestive apparatus; as a German naturalist has remarked, they devote themselves entirely to the "Minnedienst," and are to be reckoned among the few realizations of the Byronic ideal of a lover. Finally, amidst the lowest forms of animal life, the speck of gelatinous protoplasm, which constitutes the whole body, has no permanent digestive cavity or mouth, but takes in its food anywhere; and digests, so to speak, all over its body.

But although Cuvier's leading diagnosis of the animal from the plant will not stand a strict test, it remains one of the most constant of the distinctive characters of animals. And if we substitute for the possession of an alimentary cavity, the power of taking solid nutriment into the body and there digesting it, the definition so changed will cover all animals except certain parasites, and the few and exceptional cases of non-parasitic animals which do not feed at all. On the other hand, the definition thus amended will exclude all ordinary vegetable organisms.

Cuvier himself practically gives up his second distinctive mark when he admits that it is wanting in the simpler animals.

The third distinction is based on a completely erroneous conception of the chemical differences and resemblances between the constituents of animal and vegetable organisms, for which Cuvier is not responsible, as it was current among contemporary chemists.

It is now established that nitrogen is as essential a constituent of vegetable as of animal living matter; and that the latter is, chemically speaking, just as complicated as the former. Starchy substances, cellulose and sugar, once supposed to be exclusively confined to plants, are now known to be regular and normal products of animals. Amylaceous and saccharine substances are largely manufactured, even by the highest animals; cellulose is widespread as a constituent of the skeletons of the lower animals; and it is probable that amyloid substances are universally present in the animal organism, though not in the precise form of starch.

Moreover, although it remains true that there is an inverse relation between the green plant in sunshine and the animal, in so far as, under these circumstances, the green plant decomposes carbonic acid and exhales oxygen, while the animal absorbs oxygen and exhales carbonic acid; yet the exact investigations of the modern chemical investigator of the physiological processes of plants have clearly demonstrated the fallacy of attempting to draw any general distinction between animals and vegetables on this ground. In fact the difference vanishes with the sunshine, even in the case of the green

plant; which, in the dark, absorbs oxygen and gives out carbonic acid like any animal. While those plants, such as the fungi, which contain no chlorophyll and are not green, are always, so far as respiration is concerned, in the exact position of animals. They absorb oxygen and give out carbonic acid.

Thus, by the progress of knowledge, Cuvier's fourth distinction between the animal and the plant has been as completely invalidated as the third and second; and even the first can be retained only in a modified form and subject to exceptions.

But has the advance of biology simply tended to break down old distinctions, without establishing new ones?

With a qualification, to be considered presently, the answer to this question is undoubtedly in the affirmative. The famous researches of Schwann and Schleiden in 1837 and the following years, founded the modern science of histology, or that branch of anatomy which deals with the ultimate visible structure of organisms, as revealed by the microscope; and from that day to this the rapid improvement of methods of investigation, and the energy of a host of accurate observers, have given greater and greater breadth and firmness to Schwann's great generalization, that a fundamental unity of structure obtains in animals and plants; and that however diverse may be the fabrics, or *tissues*, of which their bodies are composed, all these varied structures result from the metamorphoses of morphological units (termed *cells*, in a more general sense than that in which the word "cells" was at first employed), which are not only similar in animals and in plants respectively, but present a close fundamental resemblance when those of animals and those of plants are compared together.

The contractility which is the fundamental condition of locomotion, has not only been discovered to exist far more widely among plants than was formerly imagined, but in plants, the act of contraction has been found to be accompanied, as Dr. Burdon Sanderson's interesting investigations have shown, by a disturbance of the electrical state of the contractile substance comparable to that which was found by Du Bois Reymond to be a concomitant of the activity of ordinary muscle in animals.

Again, I know of no test by which the reaction of the leaves of the Sundew and of other plants to stimuli, so fully and carefully studied by Mr. Darwin, can be distinguished from those acts of contraction following upon stimuli, which are called "reflex" in animals.

On each lobe of the bilobed leaf of Venus's fly trap (*Dionœa muscipula*) are three delicate filaments which stand out at right angles

from the surface of the leaf. Touch one of them with the end of a fine human hair and the lobes of the leaf instantly close together[1] in virtue of an act of contraction of part of their substance, just as the body of a snail contracts into its shell when one of its "horns" is irritated.

The reflex action of the snail is the result of the presence of a nervous system in that animal. A molecular change takes place in the nerve of the tentacle, is propagated to the muscles by which the body is retracted, and causing them to contract, the act of retraction is brought about. Of course the similarity of the acts does not necessarily involve the conclusion that the mechanism by which they are effected is the same; but it suggests a suspicion of their identity which needs careful testing.

The results of recent inquiries into the structure of the nervous system of animals converge towards the conclusion that the nerve fibres, which we have hitherto regarded as ultimate elements of nervous tissue, are not such, but are simply the visible aggregations of vastly more attenuated filaments, the diameter of which dwindles down to the limits of our present microscopic vision, greatly as these have been extended by modern improvements of the microscope; and that a nerve is, in its essence, nothing but a linear tract of specially modified protoplasm between two points of an organism—one of which is able to affect the other by means of the communication so established. Hence it is conceivable that even the simplest living being may possess a nervous system. And the question whether plants are provided with a nervous system or not, thus acquires a new aspect, and presents the histologist and physiologist with a problem of extreme difficulty, which must be attacked from a new point of view and by the aid of methods which have yet to be invented.

Thus it must be admitted that plants may be contractile and locomotive; that while locomotive, their movements may have as much appearance of spontaneity as those of the lowest animals; and that many exhibit actions comparable to those which are brought about by the agency of a nervous system in animals. And it must be allowed to be possible that further research may reveal the existence of something comparable to a nervous system in plants. So that I know not where we can hope to find any absolute distinction between animals and plants, unless we return to their mode of nutrition, and inquire whether certain differences of a more occult character than those imagined to exist by Cuvier, and which certainly hold good for the vast majority of animals and plants, are of universal application.

A bean may be supplied with water in which salts of ammonia

[1] Darwin, *Insectivorous Plants*, p. 289.

and certain other mineral salts are dissolved in due proportion; with atmospheric air containing its ordinary minute dose of carbonic acid; and with nothing else but sunlight and heat. Under these circumstances, unnatural as they are, with proper management, the bean will thrust forth its radicle and its plumule; the former will grow down into roots, the latter grow up into the stem and leaves of a vigorous bean plant; and this plant will, in due time, flower and produce its crop of beans, just as if it were grown in the garden or in the field.

The weight of the nitrogenous protein compounds, of the oily, starchy saccharine and woody substances contained in the full-grown plant and its seeds, will be vastly greater than the weight of the same substances contained in the bean from which it sprang. But nothing has been supplied to the bean save water, carbonic acid, ammonia, potash, lime, iron, and the like, in combination with phosphoric, sulphuric and other acids. Neither protein, nor fat, nor starch, nor sugar, nor any substance in the slightest degree resembling them have formed part of the food of the bean. But the weights of the carbon, hydrogen, oxygen, nitrogen, phosphorus, sulphur, and other elementary bodies contained in the bean plant, and in the seeds which it produces, are exactly equivalent to the weights of the same elements which have disappeared from the materials supplied to the bean during its growth. Whence it follows that the bean has taken in only the raw materials of its fabric and has manufactured them into bean stuffs.

The bean has been able to perform this great chemical feat by the help of its green colouring matter, or chlorophyll, which, under the influence of sunlight, has the marvellous power of decomposing carbonic acid, setting free the oxygen and laying hold of the carbon which it contains. In fact the bean obtains two of the absolutely indispensable elements of its substance from two distinct sources; the watery solution, in which its roots are plunged, contains nitrogen but no carbon; the air, to which the leaves are exposed, contains carbon, but its nitrogen is in the state of a free gas, in which condition the bean can make no use of it;[1] and the chlorophyll is the apparatus by which the carbon is extracted from the atmospheric carbonic acid —the leaves being the chief laboratories in which this operation is effected.

The great majority of conspicuous plants are, as everybody knows, green; and this arises from the abundance of their chlorophyll. The few which contain no chlorophyll and are colourless,

[1] I purposely assume that the air with which the bean is supplied in the case stated conains no ammoniacal salts.

are unable to extract the carbon which they require from atmospheric carbonic acid, and lead a parasitic existence upon other plants; but it by no means follows, often as the statement has been repeated, that the manufacturing power of plants depends on their chlorophyll, and its interaction with the rays of the sun. On the contrary, it is easily demonstrated, as Pasteur first proved, that the lowest fungi, devoid of chlorophyll, or of any substitute for it, as they are, nevertheless possess the characteristic manufacturing powers of plants in a very high degree. Only it is necessary that they should be supplied with a different kind of raw material, as they cannot extract carbon from carbonic acid, they must be furnished with something else that contains carbon. Tartaric acid is such a substance; and if a single spore of the commonest and most troublesome of moulds—*Penicillium*—be sown in a saucer full of water, in which tartrate of ammonia, with a small percentage of phosphates and sulphates is contained, and kept warm, whether in the dark or exposed to light, it will, in a short time, give rise to a thick crust of mould, which contains many million times the weight of the original spore, in protein compounds and cellulose. Thus we have a very wide basis of fact for the generalization that plants are essentially characterized by their manufacturing capacity—by their power of working up mere mineral matters into complex organic compounds.

Contrariwise, there is a no less wide foundation for the generalization that animals, as Cuvier puts it, depend directly or indirectly upon plants for the materials of their bodies; that is, either they are herbivorous, or they eat other animals which are herbivorous.

But for what constituents of their bodies are animals thus dependent upon plants? Certainly not for their horny matter; nor for chondrin, the proximate chemical element of cartilage; nor for gelatine; nor for syntonin, the constituent of muscle; nor for their nervous or biliary substances; nor for their amyloid matters; nor, necessarily, for their fats.

It can be experimentally demonstrated that animals can make these for themselves. But that which they cannot make, but must, in all known cases, obtain directly or indirectly from plants, is the peculiar nitrogenous matter protein. Thus the plant is the ideal *prolétaire* of the living world, the worker who produces; the animal, the ideal aristocrat, who mostly occupies himself in consuming, after the manner of that noble representative of the line of Zähdarm, whose epitaph is written in *Sartor Resartus*.

Here is our last hope of finding a sharp line of demarcation between

plants and animals ; for, as I have already hinted, there is a border territory between the two kingdoms, a sort of no-man's land, the inhabitants of which certainly cannot be discriminated and brought to their proper allegiance in any other way.

Some months ago, Professor Tyndall asked me to examine a drop of infusion of hay, placed under an excellent and powerful microscope, and to tell him what I thought some organisms visible in it were. I looked and observed, in the first place, multitudes of *Bacteria* moving about with their ordinary intermittent spasmodic wriggles. As to the vegetable nature of these there is now no doubt. Not only does the close resemblance of the *Bacteria* to unquestionable plants, such as the *Oscillatoriæ*, and lower forms of *Fungi*, justify this conclusion, but the manufacturing test settles the question at once. It is only needful to add a minute drop of fluid containing *Bacteria*, to water in which tartrate, phosphate, and sulphate of ammonia are dissolved ; and, in a very short space of time, the clear fluid becomes milky by reason of their prodigious multiplication, which, of course, implies the manufacture of living Bacterium-stuff out of these merely saline matters.

But other active organisms, very much larger than the *Bacteria*, attaining in fact the comparatively gigantic dimensions of $\frac{1}{3000}$ of an inch or more, incessantly crossed the field of view. Each of these had a body shaped like a pear, the small end being slightly incurved and produced into a long curved filament, or *cilium*, of extreme tenuity. Behind this, from the concave side of the incurvation, proceeded another long cilium, so delicate as to be discernible only by the use of the highest powers and careful management of the light. In the centre of the pear-shaped body a clear round space could occasionally be discerned, but not always ; and careful watching showed that this clear vacuity appeared gradually, and then shut up and disappeared suddenly, at regular intervals. Such a structure is of common occurrence among the lowest plants and animals, and is known as a *contractile vacuole*.

The little creature thus described sometimes propelled itself with great activity, with a curious rolling motion, by the lashing of the front cilium, while the second cilium trailed behind ; sometimes it anchored itself by the hinder cilium and was spun round by the working of the other, its motions resembling those of an anchor buoy in a heavy sea. Sometimes, when two were in full career towards one another, each would appear dexterously to get out of the other's way ; sometimes a crowd would assemble and jostle one another, with as much semblance of individual effort as a spectator on the Grands Mulets might observe

with a telescope among the specks representing men in the valley of Chamounix.

The spectacle, though always surprising, was not new to me. So my reply to the question put to me was, that these organisms were what biologists call *Monads*, and though they might be animals, it was also possible that they might, like the *Bacteria*, be plants. My friend received my verdict with an expression which showed a sad want of respect for authority. He would as soon believe that a sheep was a plant. Naturally piqued by this want of faith, I have thought a good deal over the matter; and as I still rest in the lame conclusion I originally expressed, and must even now confess that I cannot certainly say whether this creature is an animal or a plant, I think it may be well to state the grounds of my hesitation at length. But, in the first place, in order that I may conveniently distinguish this "Monad" from the multitude of other things which go by the same designation, I must give it a name of its own. I think (though for reasons which need not be stated at present, I am not quite sure) that it is identical with the species *Monas lens*, as defined by the eminent French microscopist Dujardin, though his magnifying power was probably insufficient to enable him to see that it is curiously like a much larger form of monad which he has named *Heteromita*. I shall, therefore, call it not *Monas*, but *Heteromita lens*.

I have been unable to devote to my *Heteromita* the prolonged study needful to work out its whole history, which would involve weeks, or it may be months, of unremitting attention. But I the less regret this circumstance, as some remarkable observations recently published by Messrs. Dallinger and Drysdale[1] on certain Monads, relate, in part, to a form so similar to my *Heteromita lens*, that the history of the one may be used to illustrate that of the other. These most patient and painstaking observers, who employed the highest attainable powers of the microscope and, relieving one another, kept watch day and night over the same individual monads, have been enabled to trace out the whole history of their *Heteromita*; which they found in infusions of the heads of fishes of the Cod tribe.

Of the four monads described and figured by these investigators one, as I have said, very closely resembles *Heteromita lens* in every particular, except that it has a separately distinguishable central particle or "nucleus," which is not certainly to be made out in *Heteromita lens*; and that nothing is said by Messrs. Dallinger and

[1] "Researches in the Life-history ot a Cercomonad: a Lesson in Biogenesis," and "Further Researches in the Life-history of the Monads."—*Monthly Microscopical Journal*, 873.

Drysdale of the existence of a contractile vacuole in this monad, though they describe it in another.

Their *Heteromita*, however, multiplied rapidly by fission. Sometimes a transverse constriction appeared ; the hinder half developed a new cilium, and the hinder cilium gradually split from its base to its free end, until it was divided into two ; a process which, considering the fact that this fine filament cannot be much more than $\frac{1}{100000}$ of an inch in diameter, is wonderful enough. The constriction of the body extended inwards until the two portions were united by a narrow isthmus ; finally they separated, and each swam away by itself, a complete *Heteromita*, provided with its two cilia. Sometimes the constriction took a longitudinal direction, with the same ultimate result. In each case the process occupied not more than six or seven minutes. At this rate, a single *Heteromita* would give rise to a thousand like itself in the course of an hour, to about a million in two hours, and to a number greater than the generally assumed number of human beings now living in the world in three hours ; or, if we give each *Heteromita* an hour's enjoyment of individual existence, the same result would be obtained in about a day. The apparent suddenness of the appearance of multitudes of such organisms as these in any nutritive fluid to which one obtains access, is thus easily explained.

During these processes of multiplication by fission, the *Heteromita* remains active ; but sometimes another mode of fission occurs. The body becomes rounded and quiescent, or nearly so ; and while in this resting state, divides into two portions, each of which is rapidly converted into an active *Heteromita*.

A still more remarkable phenomenon is that kind of multiplication which is preceded by the union of two monads, by a process which is termed *conjugation*. Two active *Heteromitæ* become applied to one another, and then slowly and gradually coalesce into one body. The two nuclei run into one ; and the mass resulting from the conjugation of the two *Heteromitæ* thus fused together, has a triangular form. The two pairs of cilia are to be seen, for some time, at two of the angles, which answer to the small ends of the conjoined monads ; but they ultimately vanish, and the twin organism, in which all visible traces of organisation have disappeared, falls into a state of rest. Sudden wavelike movements of its substance next occur ; and, in a short time, the apices of the triangular mass burst, and give exit to a dense yellowish, glairy fluid filled with minute granules. This process, which, it will be observed, involves the actual confluence and mixture of the substance of two distinct organisms, is effected in the space of about two hours.

The authors whom I quote say that they "cannot express" the excessive minuteness of the granules in question, and they estimate their diameter at less than $\frac{1}{200000}$ of an inch. Under the highest powers of the microscope at present applicable such specks are hardly discernible. Nevertheless, particles of this size are massive when compared to physical molecules; whence there is no reason to doubt that each, small as it is, may have a molecular structure sufficiently complex to give rise to the phenomena of life. And, as a matter of fact, by patient watching of the place at which these infinitesimal living particles were discharged, our observers assure themselves of their growth and development into new monads. These, in about four hours from their being set free, had attained a sixth of the length of the parent, with the characteristic cilia, though at first they were quite motionless; and in four hours more they had attained the dimensions and exhibited all the activity of the adult. These inconceivably minute particles are therefore the germs of the *Heteromita;* and from the dimensions of these germs it is easily shown that the body formed by conjugation may, at a low estimate, have given exit to thirty thousand of them; a result of a matrimonial process whereby the contracting parties, without a metaphor, "become one flesh," enough to make a Malthusian despair of the future of the Universe.

I am not aware that the investigators from whom I have borrowed this history have endeavoured to ascertain whether their monads take solid nutriment or not; so that though they help us very much to fill up the blanks in the history of my *Heteromita*, their observations throw no light on the problem we are trying to solve—Is it an animal or is it a plant?

Undoubtedly it is possible to bring forward very strong arguments in favour of regarding *Heteromita* as a plant.

For example, there is a Fungus, an obscure and almost microscopic mould, termed *Peronospora infestans.* Like many other Fungi, the *Peronosporæ* are parasitic upon other plants; and this particular *Peronospora* happens to have attained much notoriety and political importance, in a way not without a parallel in the career of notorious politicians, namely, by reason of the frightful mischief it has done to mankind. For it is this *Fungus* which is the cause of the potato disease; and, therefore, *Peronospora infestans* (doubtless of exclusively Saxon origin, though not accurately known to be so) brought about the Irish famine. The plants afflicted with the malady are found to be infested by a mould, consisting of fine tubular filaments, termed *hyphæ*, which burrow through the substance of the potato plant, and

appropriate to themselves the substance of their host; while at the same time, directly or indirectly, they set up chemical changes by which even its woody framework becomes blackened, sodden and withered.

In structure, however, the *Peronospora* is as much a mould as the common *Penicillium*; and just as the *Penicillium* multiplies by the breaking up of its hyphæ into separate rounded bodies, the spores; so, in the *Peranospora*, certain of the hyphæ grow out into the air through the interstices of the superficial cells of the potato plant, and develop spores. Each of these hyphæ usually gives off several branches. The ends of the branches dilate, and become closed sacs, which eventually drop off as spores. The spores falling on some part of the same potato plant, or carried by the wind to another, may at once germinate, throwing out tubular prolongations which become hyphæ, and burrow into the substance of the plant attacked. But, more commonly, the contents of the spore divide into six or eight separate portions. The coat of the spore gives way, and each portion then emerges as an independent organism, which has the shape of a bean, rather narrower at one end than the other, convex on one side, and depressed or concave on the opposite. From the depression, two long and delicate cilia proceed, one shorter than the other, and directed forwards. Close to the origin of these cilia, in the substance of the body, is a regularly pulsating contractile vacuole. The shorter cilium vibrates actively, and effects the locomotion of the organism, while the other trails behind; the whole body rolling on its axis with its pointed end forwards.

The eminent botanist, De Bary, who was not thinking of our problem, tells us, in describing the movements of these "Zoospores," that, as they swim about, "Foreign bodies are carefully avoided, and the whole movement has a deceptive likeness to the voluntary changes of place which are observed in microscopic animals."

After swarming about in this way in the moisture on the surface of a leaf or stem (which, film though it may be, is an ocean to such a fish) for half an hour, more or less, the movement of the zoospore becomes slower, and is limited to a slow turning upon its axis, without change of place. It then becomes quite quiet, the cilia disappear, it assumes a spherical form, and surrounds itself with a distinct, though delicate membranous coat. A protuberance then grows out from one side of the sphere, and, rapidly increasing in length, assumes the character of a hypha. The latter penetrates into the substance of the potato plant, either by entering a stomate or by boring through the wall of an epidermic cell, and ramifies, as a mycelium, in the substance

of the plant, destroying the tissues with which it comes in contact. As these processes of multiplication take place very rapidly, millions of spores are soon set free from a single infested plant; and from their minuteness they are readily transported by the gentlest breeze. Since, again, the zoospores set free from each spore, in virtue of their powers of locomotion, swiftly disperse themselves over the surface, it is no wonder that the infection, once started, soon spreads from field to field, and extends its ravages over a whole country.

However, it does not enter into my present plan to treat of the potato disease, instructively as its history bears upon that of other epidemics; and I have selected the case of the *Peronospora* simply because it affords an example of an organism, which, in one stage of its existence, is truly a "Monad," indistinguishable by any important character from our *Heteromita*, and extraordinarily like it in some respects. And yet this "Monad" can be traced, step by step, through the series of metamorphoses which I have described, until it assumes the features of an organism, which is as much a plant as an oak or an elm is.

Moreover it would be possible to pursue the analogy further. Under certain circumstances, a process of conjugation takes place in the *Peronospora*. Two separate portions of its protoplasm become fused together, surround themselves with a thick coat, and give rise to a sort of vegetable egg called an *oospore*. After a period of rest, the contents of the oospore break up into a number of zoospores like those already described, each of which, after a period of activity, germinates in the ordinary way. This process obviously corresponds with the conjugation and subsequent setting free of germs in the *Heteromita*.

But it may be said that the *Peronospora* is, after all, a questionable sort of plant; that it seems to be wanting in the manufacturing power selected as the main distinctive character of vegetable life; or, at any rate, that there is no proof that it does not get its protein matter ready made from the potato plant.

Let us, therefore, take a case which is not open to these objections.

There are some small plants known to botanists as members of the genus *Coleochæte*, which, without being truly parasitic, grow upon certain water-weeds, as lichens grow upon trees. The little plant has the form of an elegant green star, the branching arms of which are divided into cells. Its greenness is due to its chlorophyll, and it undoubtedly has the manufacturing power in full degree, decomposing carbonic acid and setting free oxygen under the influence of sunlight.

But the protoplasmic contents of some of the cells of which the

plant is made up occasionally divide, by a method similar to that which effects the division of the contents of the *Peronospora* spore ; and the severed portions are then set free as active monad-like zoospores. Each is oval and is provided at one extremity with two long active cilia. Propelled by these, it swims about for a longer or shorter time, but at length comes to a state of rest and gradually grows into a *Coleochæte.*

Moreover, as in the *Peronospora,* conjungation may take place and result in an oospore ; the contents of which divide and are set free as monadiform germs.

If the whole history of the zoospores of *Peronospora* and *Coleochæte* were unknown, they would undoubtedly be classed among " Monads " with the same right as *Heteromita* ; why then may not *Heteromita* be a plant, even though the cycle of forms through which it passes shows no terms quite so complex as those which occur in *Peronospora* and *Coleochæte*? And, in fact, there are some green organisms, in every respect characteristically plants, such as *Chlamydomonas,* and the common *Volvox,* or so-called " Globe animalcule," which run through a cycle of forms of just the same simple character as those of *Heteromita.*

The name of *Chlamydomonas* is applied to certain microscopic green bodies, each of which consists of a protoplasmic central substance invested by a structureless sac. The latter contains cellulose, as in ordinary plants ; and the chlorophyll which gives the green colour enables the *Chlamydomonas* to decompose carbonic acid and fix carbon, as they do. Two long cilia protrude through the cell wall, and effect the rapid locomotion of this " monad," which, in all respects, except its mobility, is characteristically a plant.

Under ordinary circumstances the *Chlamydomonas* multiplies by simple fission, each splitting into two or into four parts, which separate and become independent organisms. Sometimes, however, the *Chlamydomonas* divides into eight parts, each of which is provided with four instead of two cilia. These " zoospores " conjugate in pairs, and give rise to quiescent bodies, which multiply by division, and eventually pass into the active state.

Thus, so far as outward form and the general character of the cycle of modifications through which the organism passes in the course of its life are concerned, the resemblance between *Chlamydomonas* and *Heteromita* is of the closest description. And on the face of the matter there is no ground for refusing to admit that *Heteromita* may be related to *Chlamydomonas,* as the colourless fungus is to the green alga. *Volvox* may be compared to a hollow sphere, the wall of which

is made up of coherent Chlamydomonads; and which progresses with a rotating motion effected by the paddling of the multitudinous pairs of cilia which project from its surface. Each *Volvox*-monad has a contractile vacuole like that of *Heteromita lens*; and moreover possesses a red pigment spot like the simplest form of eye known among animals.

The methods of fissive multiplication and of conjugation observed in the monads of this locomotive globe are essentially similar to those observed in *Chlamydomonas*; and though a hard battle has been fought over it, *Volvox* is now finally surrendered to the Botanists.

Thus there is really no reason why *Heteromita* may not be a plant; and this conclusion would be very satisfactory, if it were not equally easy to show that there is really no reason why it should not be an animal.

For there are numerous organisms presenting the closest resemblance to *Heteromita*, and, like it, grouped under the general name of "Monads," which, nevertheless, can be observed to take in solid nutriment, and which therefore have a virtual, if not an actual, mouth and digestive cavity, and thus come under Cuvier's definition of an animal. Numerous forms of such animals have been described by Ehrenberg, Dujardin, H. James Clark and other writers on the *Infusoria*.

Indeed, in another infusion of hay in which my *Heteromita lens* occurred, there were innumerable infusorial animalcules belonging to the well known species *Colpoda cucullus*.[1]

Full-sized specimens of this animalcule attain a length of between $\frac{1}{300}$ or $\frac{1}{400}$ of an inch, so that it may have ten times the length and a thousand times the mass of a *Heteromita*. In shape it is not altogether unlike *Heteromita*. The small end, however, is not produced into one long cilium, but the general surface of the body is covered with small actively vibrating ciliary organs, which are only longest at the small end. At the point which answers to that from which the two cilia arise in *Heteromita*, there is a conical depression, the mouth; and in young specimens a tapering filament, which reminds one of the posterior cilium of *Heteromita*, projects from this region.

The body consists of a soft granular protoplasmic substance, the middle of which is occupied by a large oval mass called the "nucleus;" while, at its hinder end, is a "contractile vacuole," conspicuous by its regular rhythmic appearances and disappearances. Obviously, although the *Colpoda* is not a monad, it differs from one only in

[1] Excellently described by Stein, almost all of whose statements I have verified.

subordinate details. Moreover, under certain conditions, it becomes quiescent, incloses itself in a delicate case or *cyst*, and then divides into two, four, or more portions, which are eventually set free and swim about as active *Colpodæ*.

But this creature is an unmistakable animal, and full-sized *Colpodæ* may be fed as easily as one feeds chickens. It is only needful to diffuse very finely ground carmine through the water in which they live, and, in a very short time, the bodies of the *Colpodæ* are stuffed with the deeply coloured granules of the pigment.

And if this were not sufficient evidence of the animality of *Colpoda*, there comes the fact that it is even more similar to another well-known animalcule, *Paramæcium*, than it is to a monad. But *Paramæcium* is so huge a creature compared with those hitherto discussed—it reaches $\frac{1}{120}$ of an inch or more in length—that there is no difficulty in making out its organization in detail; and in proving that it is not only an animal, but that it is an animal which possesses a somewhat complicated organization. For example, the surface layer of its body is different in structure from the deeper parts. There are two contractile vacuoles, from each of which radiates a system of vessel-like canals; and not only is there a conical depression continuous with a tube, which serve as mouth and gullet, but the food ingested takes a definite course and refuse is rejected from a definite region. Nothing is easier than to feed these animals and to watch the particles of indigo or carmine accumulate at the lower end of the gullet. From this they gradually project, surrounded by a ball of water, which at length passes with a jerk, oddly simulating a gulp, into the pulpy central substance of the body, there to circulate up one side and down the other, until its contents are digested and assimilated. Nevertheless, this complex animal multiplies by division, as the monad does, and, like the monad, undergoes conjugation. It stands in the same relation to *Heteromita* on the animal side, as *Coleochæte* does on the plant side. Start from either, and such an insensible series of gradations leads to the monad that it is impossible to say at any stage of the progress—here the line between the animal and the plant must be drawn.

There is reason to think that certain organisms which pass through a monad stage of existence, such as the *Myxomycetes*, are, at one time of their lives, dependent upon external sources for their protein-matter, or are animals; and at another period manufacture it or are plants. And seeing that the whole progress of modern investigation is in favour of the doctrine of continuity, it is a fair and probable speculation—though only a speculation—that, as there are

some plants which can manufacture protein out of such apparently intractable mineral matters as carbonic acid, water, nitrate of ammonia, and metallic salts; while others need to be supplied with their carbon and nitrogen in the somewhat less raw form of tartrate of ammonia and allied compounds; so there may be yet others, as is possibly the case with the true parasitic plants, which can only manage to put together materials still better prepared—still more nearly approximated to protein—until we arrive at such organisms as the *Psorospermiæ* and the *Panhistophyton*, which are as much animal as vegetable in structure, but are animal in their dependence on other organisms for their food.

The singular circumstance observed by Meyer, that the *Torula* of yeast, though an indubitable plant, still flourishes most vigorously when supplied with the complex nitrogenous substance, pepsin; the probability that the *Peronospora* is nourished directly by the protoplasm of the potato plant; and the wonderful facts which have recently been brought to light respecting insectivorous plants, all favour this view; and tend to the conclusion that the difference between animal and plant is one of degree rather than of kind; and that the problem whether, in a given case, an organism is an animal or a plant, may be essentially insoluble.

XII

ON THE EVIDENCE AS TO THE ORIGIN OF EXISTING VERTEBRATE ANIMALS.[1]

Nature, vol. xiii., 1876, *pp.* 388–389, 410–412, 429–430, 467–469, 514–516
vol. xiv., 1876, *pp.* 33–34.

I

TWENTY years ago the arguments as to the causes of the phenomena of organic nature, brought forward in support of the then recently advanced views of Mr. Darwin, were largely speculative; all one could hope to show was that no valid objections could be urged against the theory of evolution. But since that time "many have run to and fro and knowledge has been increased"; the question has come out of the region of speculation into that of proof; every day increases our familiarity with the phenomena of life on the globe in antecedent ages, and so gives us the only valid evidence obtainable as to the evolution of living things.

When we consider any animal at the present day there are three hypotheses which may be put forward with regard to its origin: that it arose out of nothing, that it had its origin from dead inorganic matter, or that it arose as a modification of some pre-existing living being. It is hardly worth while to consider the two first of these hypotheses—for the first it would be utterly impossible to obtain any evidence, and the second is devoid of all ground of analogy, and opposed to all our knowledge of what actually takes place. The last, on the other hand, should, if true, be capable of some sort of proof—at any rate it can be brought to the test of facts.

It is quite conceivable that all evidence as to the origin of an animal may have disappeared, and that the problem becomes, in

[1] A course of six lectures to working men, delivered in the theatre of the Royal School of Mines. Lecture I., Feb. 28, 1876.

consequence, insoluble by direct evidence, analogy and probability being the only guides left. As a matter of fact, however, we possess in the 70,000 feet of stone, gravel, sand, &c., which form the earth's crust, fossil remains imbedded in chronological order, and in many cases so perfectly preserved, that all important details can be made out almost as well as in the recent state.

The plan adopted in these lectures will be not to give all obtainable evidence with regard to the origin of each group of vertebrate animals, but to select from each class one or two definite cases of living animals, and to see what evidences can be obtained, by going back in time, as to the way in which they have come about, or at any rate as to the extent of the duration of their existence.

To begin with fishes: we will take as our first example the very beautiful genus Beryx, a fish not unlike our sea-bream, found widely distributed through the deep seas, and extending to about 40° on each side of the equator. Like the perch or the sea-bream, it is a greatly *specialised* fish; the head is immensely large, the bony rays supporting the fins hard and unjointed, the ventral fins or representatives of the hind limbs situated just behind the head, under the throat, the operculum curiously ornamented, and the air-bladder completely shut off from the gullet; thus differing very markedly from a more *generalised* fish such as the herring or carp, in which the head is proportionally much smaller, the fin-rays soft and jointed, the ventral fins far back, the operculum not ornamented, and the air-bladder communicating by a duct with the œsophagus.

We now know that at depths greater than five or six hundred fathoms, the sea-bottom is to a great extent composed of a very fine greyish-white mud, sticky when first removed from the water, but afterwards hardening into a delicate friable stone, not at all unlike chalk. This mud, which is largely made up of shells of the minute marine organism *Globigerina*, forms the bed of thousands of square miles of sea in which Beryx lives, and there can be no doubt that when the fish dies it sinks to the bottom, and, its soft parts being destroyed, becomes gradually imbedded in the soft mud, there to remain until the present sea-bottom is upheaved and becomes dry land.

Now, as a matter of archæological evidence, what is known of the history of Beryx and of the source whence it proceeded? Naturally it is useless to seek for such evidence except in deposits formed under like conditions to those in which the fish lives at the present day. Through the whole of the Pliocene and Miocene epochs no deep-sea formations are known, but in the middle of the Eocene

period—a time so remote that tropical plants flourished on the banks of the Thames, and crocodiles abounded in this country—we are acquainted with an extensive deep-sea deposit, the Nummulitic limestone, which, besides the fossil giving it its name, contains large quantities of Globigerina, in all essential respects like that of the present day. In this formation are found two forms closely allied to Beryx, but with such slight differences as to receive different generic names; these are known as Acanus and Pristigaster. On passing from the Eocene or lowest tertiary to the chalk or uppermost secondary formation, which bears the closest possible resemblance to the modern Atlantic mud—the two may, in fact, be looked upon as belonging to one continuous series of deposits—we find an actual Beryx, a fish differing no more from the modern Berices than the various modern species of Beryx do from one another. This fossil, owing to the fineness of the chalk-forming mud in which it was buried, is so perfectly preserved, that all the details of structure of its hard parts, even to the ornamentation of the scales, can be compared with those in the recent fish; and in this way the most conclusive evidence is obtained that the differences which separate it from its modern relatives are of no greater importance than those by which the recent species of Beryx are distinguished from one another.

Thus we have positive evidence that a fish altogether like the Beryx of the present day, existed millions of years ago, before the Alps, the Himalayas, or the Rocky Mountains were upheaved, and has continued to live ever since. In face of these facts we cannot but conclude that the modern Beryx is derived from that of the chalk, and that the hypotheses of its creation out of nothing, and of its origin from inorganic matter are, for scientific purposes, simply non-existant.

As to the form from which the Beryx of the chalk was derived we have absolutely no evidence, for there is no trace of any such fish in any lower formation.

We now pass on to a fish of a far older and less specialised type than Beryx—the genus *Ceratodus*, recently discovered in Australia. This animal, which attains a length of six feet, is distinguished by the possession of very curious fins, consisting of a central lobe with a surrounding fringe of fin-rays, and by the character of its teeth, which are produced into curious horn-like processes, so arranged that those of opposite jaws interlock. Ceratodus is probably a vegetable feeder, lives in fresh or brackish water, and is said sometimes to leave its native element and crawl about among the weeds on the bank. It is enabled to do this by

the fact that it can breathe air directly as well as air dissolved in water; it has, in fact, besides gills, an organ which is altogether a half-way house between the air-bladder of a fish and the lung of an amphibian.

In the Wealden, the most recent estuarine deposit of which we have any knowledge, there is no trace of Ceratodus to be found, but this is hardly surprising, as only two or three small patches of the earth's surface formed at this epoch have been examined, and animals have a geographical distribution at all times. But on passing back to the Trias, a formation as far from the chalk in point of time as the chalk from the present day, we find teeth belonging to an undoubted Ceratodus, in shape and in microscopic structure, exactly like those of the modern Australian fish. No other remains of the Triassic Ceratodus have as yet been found, but teeth are known to be so important a diagnostic character that no naturalist would have any hesitation in naming the genus to which the fish bearing such teeth should be assigned.

Thus we have a far more astonishing example of a persistent type than was afforded by our Beryx, and as in the case of the latter fish, all trace of the actual genus Ceratodus is lost at this point, and we are obliged to content ourselves with a few singular hints as to the way in which the type has come about. The most valuable of these hints are obtained by a study of a singular group of fish found in great abundance in the Old Red Sandstone. These are distinguished by the possession of curious fringed fins, unlike those of any other fish, except Lepidosiren and Ceratodus—in fact, one genus, Dipterus, has fins quite like those of Ceratodus, and its teeth and skeleton were formed on just the same type. It is doubtful whether there is any relation between Ceratodus and Dipterus in the way of ancestry, but the resemblance between them is remarkable.

It must seem rather strange for a known evolutionist to select as examples two fish like Beryx and Ceratodus, which, of all others, seem most likely to support the notion that species are immutable. The adverse side only of the question has been stated to-night, the other side will be treated of on future occasions.

II[1]

It was seen in the last lecture that no ultimate answer was obtainable as to the origin of the examples selected from the fish class, any more than is afforded as to the origin of the Anglo-Saxons

[1] Delivered March 6, 1876.

by showing that they came from Friesland in the sixth or seventh century. The same remark applies to the origin of nearly all fishes, in fact, only one clear case of progressive modification is known in the whole class ; this is afforded by the group of the *Pycnodonta.*

These are fish not unlike our John Dory in shape, which appear for the first time in the carboniferous rocks, and become extinct in the older tertiaries ; they are distinguished by the possession of rows of large crushing teeth, and in place of a vertebral column had a gelatinous *chorda dorsalis* or *notochord.* The spinal cord above this was embraced by arches of bone, placed at regular intervals along the chorda ; and, immediately below these neural arches, were attached the ribs also bony. In the Carboniferous forms, both arches and ribs are quite distinct from one another, and are simply united by ligamentous fibres to the notochord ; but, in the older Secondary species, they become expanded at their ends, and thus tend to embrace the notochord ; and, lastly, in the Tertiary pycnodonts this process is carried to such an extent as almost to produce a ring of bone, like the body of a rudimentary vertebra.

Now let us turn to the next group of Vertebrate animals, that of Amphibia (frogs, toads, newts, and salamanders), which are distinguished from fishes by certain very striking peculiarities. Fishes are all capable of breathing the air dissolved in water by means of gills, and—a far more important distinctive character—their limbs always have the character of *fins*, which organs are seen in their simplest form in Ceratodus. In this fish, there is a long jointed cartilaginous axis, running down the middle of the fin, with rows of rays of the same substance on each side of it ; the whole is invested by a fold of the integument, the margins of which are beset with horny filaments called fin-rays. In all fishes these elements are to be found, generally in a curiously modified condition ; in the bony fishes, for instance, the central axis with its side appendages are broadened out and shortened, the fin-rays becoming at the same time so much larger as to form the main part of the fin.

Some modification of this type of limb is possessed by all fishes which have limbs at all ; but the first character, that afforded by the respiratory organs, is not absolute, for there are some fishes which, besides gills, possess an apparatus for breathing air directly. This apparatus, represented by the air-bladder of ordinary fishes, first takes on its new character, and becomes a lung in that remarkable genus, Ceratodus, in which it exists as a large cellular structure situated in the upper part of the abdominal cavity, just under the vertebral column, and connected with the gullet by a slit—

the glottis—by means of which the fish can pass air from the mouth into the lung. It is not, however, this peculiarity of opening into the œsophagus which constitutes a lung, for the air-bladder of many fishes possesses an open duct of a similar nature; the great distinguishing feature is, that the blood taken to this bladder does not pass into the ordinary venous channels, but is returned immediately to the heart, in a purified condition, by a special vein. In Ceratodus there is no special vessel to carry blood *to* the lung, in other words, although there is a pulmonary *vein*, the pulmonary *artery* has not appeared; but in the Mudfish (Lepidosiren) of Africa and eastern South America, the development of the lung goes a step further, a special pulmonary artery being present, as in all the higher animals. Thus Ceratodus and Lepidosiren are truly *amphibious*, for they can be suffocated neither by removal from water like most fish, nor by immersion in water like the higher animals.

What constitutes the difference between these amphibious fish, and the lowest of the true Amphibia? Not the nature of the respiratory process, for many of the latter group, such as the blind Proteus of the Austrian caves and the North American Menobranchus possess gills throughout life, but the structure of the limbs, which are now, no longer *fins*, but *legs*. A fish requires a broad surface for balancing itself in the water, locomotion being chiefly performed by the tail, but in land animals an apparatus is required capable of raising the body above the ground, and the limbs take on the form of a set of jointed levers. In its simplest form the higher vertebrate limb, consists, first, of a single piece of cartilage articulated with the body, then two pieces side by side, then a number of small nodules, and lastly, five series of short jointed pieces; all of these become in the adult state more or less converted into bone. The first or proximal division of the limb is called the humerus in the fore limb, the femur in the hind limb; the next segment consists of radius and ulna in the arm, tibia and fibula in the leg; the nodular pieces are respectively carpals and tarsals, and the series of jointed bones or cartilages, the five digits. From the lowest Amphibia upwards, the limbs, when present, are always constructed upon this type.

Nevertheless, the Amphibia still retain certain fish-like characters, which are lost in the groups above them. They all, at some period of life, breathe by means of gills, although all have, in the adult state, lungs in addition. Some forms, such as the Proteus and Menobranchus mentioned above, retain their gills throughout life and are hence called *Perennibranchiates*; others, such as Menopoma,

Amphiuma, &c., lose them in adult life, and are called *Caducibranchiates*. These two last genera, however, still retain traces of gill-clefts; but in all the Amphibia with which we are acquainted in this country, the frog, toad, and newt, even the clefts disappear, and the perfect air-breathing character is assumed.

These animals, in the course of their development, go through a very singular series of metamorphoses, comparable to those by which a grub is converted into a butterfly. At this season of the year, every pond is almost certain to contain frog-spawn, masses of transparent albuminous matter, with numberless imbedded eggs, consisting of yolk, black on one side and white on the other. A few hours after these eggs are laid, the process of development begins by the formation of a shallow groove, which appears quickly on the black, more slowly on the white hemisphere, and is just such a groove as would be produced by drawing a blunt instrument along the equator of a soft globe. The egg is thus divided into two masses. A second form appears at right angles to the first, dividing the whole egg into four; others appear, in definite order, cutting it up into smaller and smaller masses, until the whole yolk becomes granular, or formed of microscopic *cells*. Two ridges then appear, on the surface of the egg, and, uniting in the middle line, enclose a cavity, the lining membrane of which is converted into the brain and spinal cord. The head gradually becomes differentiated, and the mouth appears on its under side; the tail grows out, and the little creature, getting too long for the egg, becomes coiled upon itself, and before long, ruptures the egg-membrane, and makes its exit from its mass of jelly.

It is now, to all intents and purposes, a fish; it has no limbs, its mouth is provided with horny jaws, and it breathes by means of a pair of plumose gills. It further differs from the adult frog in being herbivorous, feeding on water plants, to which it attaches itself by means of two suckers near the mouth. The tadpole grows rapidly, and, before long, a fold of skin appears on each side, which gradually closes over the gills, leaving, however, for a considerable time, a small opening on the left side. In the meantime the limbs appear, and the lungs are developed, the tadpole breathing for a time both by lungs and gills; the latter eventually disappear, the tail shortens, the limbs lengthen, the horny jaws are replaced by teeth, and an insect-eating tail-less frog is formed, the adult air-breathing form having thus been attained by a wonderful series of changes, in which the fish, Lepidosiren, perennibranchiate, and triton, are all represented.

One would be inclined to infer from these metamorphoses, that, on tracing the Amphibia back in time, the story of their origin should be told, but, as a matter of fact, palæontological history tells a different story altogether. Abundant remains of frogs and toads are found in the Miocene deposits, some of which are of so fine a character that even the tadpoles are preserved; but these tertiary frogs and toads do not differ, in any important particulars, from those of the present day, and the same is true of the tritons and salamanders. Some of the latter attained a very great size, and one of them—a near ally of the great Japanese salamander of the present day—has had a very singular fate, having been described, about the middle of the last century, as a fossil man, by the German naturalist Scheuchzer, who named it "Homo diluvii testis," the man who saw the flood!

In the Wealden and Purbeck formations no Amphibia have as yet been discovered, but, from the Lower Lias to the Carboniferous they turn up again in remarkable numbers, and of great size, but differing from existing forms in some important peculiarities, and affording no help whatever to our inquiries as to the origin of the existing or of the tertiary frogs, toads, and salamanders. Under the throat, these gigantic Amphibia had a remarkable shield of three bony plates, as well as a series of plates along the belly. Their teeth were large and powerful, and presented an extremely complicated structure, whence the group has received its name of *Labyrinthodonta.*

Thus, in tracing back the existing Amphibia, we find a great break in the secondary period, and then come upon a distinct group, the Labyrinthodonta, from which the existing forms cannot possibly be deduced. These, again, have been traced no farther back than the carboniferous epoch.

III[1]

It will be necessary to preface our remarks as to the origin of the next highest group of Vertebrates—that of Reptiles—by some account of the distinction between them and the Amphibia, and by some observations on what zoologists mean by the terms "higher" and "lower" as applied to animals or groups of animals.

In external form there is little difference between such a reptile as a lizard, and such an amphibian as a newt, and there seems, at first sight, to be no reason why they should be placed in different primary groups. In former times, as a matter of fact, the essential

[1] Delivered March 13, 1876.

difference between reptiles and amphibians was not seen, and the two were united into a single class; but modern researches have shown that, beneath this external similarity, lie great and important differences, the chief of which we must now consider.

In the first place, no reptile, at any period of its life, possesses gills, and, in consequence, the breathing of air dissolved in water becomes impossible. Nevertheless, reptiles, in common with all the higher animals, have, at one period in their existence, slits leading from the throat to the exterior, in precisely the same position as the branchial clefts of an amphibian, but functionless.

Secondly, certain organs, known as "fœtal appendages," are developed in connection with the young animal before it leaves the egg, and serve a temporary purpose in its economy. In the possession of these appendages, as well as in the absence of gills, reptiles agree with birds and mammals, and differ from fishes and amphibians.

The young reptile is produced from an egg of relatively large size, and consisting of a considerable mass of yolk, surrounded by a quantity of transparent "white" or albumen; the whole being invested by a hard or soft shell. The yolk does not divide as a whole, but the process of division is confined to a small patch on its surface; in fact, the reptilian egg answers to the amphibian egg, *plus* a quantity of additional matter, called accessory, or food-yolk, which is unaffected by the process of yolk-division. It is the small superficial patch, answering to the whole amphibian egg, which is converted into the body of the young reptile, the accessory yolk becoming gradually smaller and smaller, as its substance is used up in the nourishment of the embryo; in the meantime it forms a bag attached to the umbilicus of the embryo, and hence called the *umbilical vesicle* or yolk-sac; it is the first of the fœtal appendages, and the only one which occurs in any vertebrate below a reptile, being possessed by certain fishes.

After the embryo has attained a certain size, and has come to lie, like an inverted boat, on the yolk-sac, a fold grows up, all round it, from the surface of the yolk, and, the edges of the fold coming together above, a bag is formed enclosing the embryo into the interior of which a watery fluid is secreted, in which the little creature lies. This natural water-bed is called the *amnion*; it is the second of the fœtal appendages, and no trace of it is to be found in any fish or amphibian.

The third and last of these curious embryonic appendages, the *allantois*, grows out from the tail-end of the embryo as a pear-shaped body, solid at first, but soon converted into a sac, which extends round the embryo and yolk-sac, immediately beneath the membrane

of the shell. The cavity of the allantois acts as a receptacle for the nitrogenous waste of the embryonic body, but its chief function is as a respiratory organ ; for this purpose it is supplied by blood-vessels which form a close network over its outer layer, and the blood contained in these coming into close relation with the external air, through the porous shell, readily exchanges its carbonic acid for the atmospheric oxygen.

As the embryo grows, the yolk-sac becomes smaller and smaller, and is eventually completely drawn into the interior of the body of the young reptile, which by this time completely fills the shell. In many cases a horny knob is developed on the nose, and with this, the now ripe embryo breaks the shell from the interior ; the amnion and other membranes are burst, the allantoic circulation is stopped, the first inspiration is taken, and the little creature is born.

There are several minor points in which reptiles are distinguished from amphibia, amongst which we will only mention the articulation of the skull to the first vertebra by one condyle instead of two, the presence of a bone called the *basi-occipital* in the hinder part of the skull floor, and the fact that the branchial apparatus is reduced in the adult to the small *hyoid* bone or cartilage, which supports the tongue.

In what respects is a reptile a higher organism than an amphibian ? When one animal is said to be higher than another, one of two things may be meant : its structure may be more complicated, as a carved platter is higher than a simple trencher ; or its parts may be so arranged as to form a more complicated mechanism. The mere repetition of parts does not raise an animal in the scale ; a worm with a hundred segments is no higher than one with ten, any more than a mill with ten pairs of stones is a higher kind of machine than one with a single pair. But if, instead of multiplying the number of millstones, two pairs only were used, one of which was adapted for coarse, the other for fine grinding, a machine of a far higher order would be produced, and it is a similar differentiation of parts for special uses and co-adaptation of structures to given purposes which raises an animal above its fellows.

Judged by this standard, a reptile is a decidedly higher animal than an amphibian ; its skeleton, for instance, is a better piece of work, the joints being more neatly finished, and the whole mechanism much more perfect.

A third test is based on the facts of development. We saw that a frog, in the course of its development, went through a stage

in which it was, to all intents and purposes, a fish, and that it was only after passing through this stage, as well as that of a branchiate amphibian, that it attained its higher adult character. Now the reptile stands in just the same relation to the amphibian, with regard to its development, as the amphibian to the fish. During the earlier stage of its growth it presents certain amphibian characters, such as the presence of gill-clefts ; but these lower stages are passed over ; the reptile goes beyond the highest amphibian in its development, and is therefore, in this respect also, to be considered as a higher animal.

At the present day there are four types of reptiles : the lizards (*Laartilia*), snakes (*Ophidia*), turtles and tortoises (*Chelonia*), and crocodiles (*Crocodilia*). We will now direct our attention to the first of these groups.

Most existing lizards have four well developed limbs, a long tail, a scaly armour, sometimes supplemented with plates of bone, and teeth, not set in distinct sockets, but firmly fixed to the jaw. The skull is so constructed that the hinder nostrils open far forwards into the mouth. The vertebræ have a peculiar and characteristic form, their articular surfaces being concave in front and convex behind, except in the Geckos or wall-lizards, and that remarkable New Zealand genus *Hatteria* or *Sphenodon*. The heart is composed of three chambers, two auricles and a single ventricle, the latter being again partly divided into two, and thus showing a slight advance on the amphibian heart, in which the ventricle is quite single.

Lizards are very abundant, especially in hot climates ; most of them are land animals, a few only being inhabitants of fresh water, and one—the genus *Amblyrhynchus* of the Galapagos Archipelago—lives on the seashore, and, if hard pressed, takes to the sea.

Through the whole of the Tertiary epoch the lizards are essentially the same as those now existing. Some of the Secondary species, also, have the same characters, but in the chalk are found, in addition, strange marine lizards, such as the genus *Mosasaurus*, which attained a length of thirty feet. As far back as the Purbecks, the lizards have vertebræ like the existing kinds, but on descending to the Solenhofen slates we find abundant remains, which present the lower character of bi-concave vertebræ, and the same is true of all the still older forms, such as the *Telerpeton* of the Triassic sandstones of Elgin and the Permian *Protorosaurus*.

Thus the older lizards have a slightly simpler structure than those of the present day, but resemble them, on the whole, so closely, that we must conclude our existing forms to have been derived from the

ancient ones, and have no need whatever to assume their special creation. Lizards, then, offer another example of what is meant by a persistent type.

A remarkable instance of this persistence is afforded by a case of quite the same order as that of Ceratodus, described in the first lecture. The Hatteria, mentioned above, differs from all other lizards in many particulars. Its jaws are armed with a horny beak, and its upper jaw has two rows of teeth, one on the maxillary, the other on the palatine bones; the teeth of the lower jaw bite between these, like a pair of scissors with a double upper blade. The vertebræ are bi-concave, and, along the belly, are placed a number of bony plates.

No other existing form whatever is known presenting these characters, but, about the year 1858, a number of fossils were discovered in the sandstone of Elgin, and amongst them the remains of a large lizard with bi-concave vertebræ, abdominal plates, a horny beak, a double row of upper jaw teeth, and, in fact, altogether like the existing Hatteria.

The crocodiles are the only other reptiles the history of which it will be possible to notice in this course. Two of the most important characters by which they are distinguished from lizards are, the lodgment of the teeth in distinct sockets and the position of the hinder nostrils or posterior nares. The maxillary, palatine, and pterygoid bones are so disposed as to form a remarkable shelf or partition in the roof of the mouth, thus bringing the posterior nares to the hindermost part of the throat. The soft palate forms a veil in front of these apertures, and hangs down so as to rest on the back part of the rudimentary tongue, and thus, except when the animal is swallowing, entirely shuts off the cavity of the mouth from the air passages. This arrangement has been prettily explained by the crocodile's habit of killing its prey by drowning; it is said that it can hold a captured animal under water, while its own nostrils—placed at the end of the long snout—are just above the surface, and thus is enabled to breathe freely, the air passing through the posterior nares, behind the veil of the palate, and so to the lungs, while its prey is being suffocated. This is an admirable explanation as far as the crocodile is concerned, but, unfortunately, it is probably untrue, for precisely the same arrangement is found in the Gavial and other crocodilians which live upon fish.

IV[1]

The crocodiles form the highest group of existing reptiles ; they are higher than lizards as a steam-vessel is higher than a sailing-ship ; for, while built essentially on the same lines, and exhibiting altogether the same fundamental structure, they are in some respects peculiarly modified, and that always in the direction of greater complexity.

Besides the characters of the skull mentioned in the last lecture, they are distinguished from lizards by having a four-chambered heart, one in which the separation of the ventricle into two distinct cavities is completed, so that, in the heart itself, the blood from the lungs is kept separate from that returned from the body generally. A mixture, however, takes place subsequently, through an aperture between the two aortæ, one of which springs from each ventricle.

Crocodiles are found in Central America, India, Africa, and Australia. Of the many species, the greater number are short-snouted ; the fish-eating Gavial of the Ganges, on the other hand, has an extremely long and narrow snout.

All the existing crocodiles are fresh-water or estuarine animals, but, fortunately, this was not the case with the ancient forms, many of which were exclusively marine, seeming, so to say, to take the place in the sea of their own epoch, of our porpoises and dolphins.

Besides Tertiary species, crocodiles are found in the Chalk, Oolite, Lias, and Trias often in the best possible state of preservation ; they therefore extend back to the very commencement of the Mesozoic epoch.

If we had specimens of all known forms of crocodiles, recent and extinct, and set to work to classify them according to their degrees of likeness and unlikeness, we should find that they naturally fell into three series.

In the first of these it would be found that the skull had all the characters mentioned at the end of the last lecture, the posterior nares being small apertures opening into the cavity of the mouth behind the pterygoid bones ; the vertebræ would be concave in front and convex behind ; the two bones composing the shoulder-girdle, the shoulder-blade or scapula and the coracoid, would be similar in shape, both being long and narrow ; in the hip-girdle, the haunch-bone or ilium would be much cut away in front and excavated below, the ischium and pubis being both long blade-like bones ; and there would be seven or eight longitudinal rows of bony plates on the back.

[1] Delivered March 20, 1876.

In the second set we should find the posterior nares to be much larger and placed farther forwards, immediately behind the palatine bones, the pterygoids not uniting as in the first group. The vertebræ would be slightly hollowed out at each end. In the shoulder and hip girdles there would be no important difference from the first group, with which also the more minute structure of the limbs would correspond closely. A difference would, however, be found in the fact of there being not more than two rows of plates on the back.

In the third series, we should notice certain very striking changes. The posterior nares would be actually as far forward as in a lizard; neither the palatine nor the pterygoids uniting in the floor of the mouth; the vertebræ would be completely amphicœlous or biconcave; the coracoid no longer long and narrow, but expanded and rounded like that of a lizard; the ilium more elongated and without the notch on its lower edge; and the ischium considerably broadened. As in the preceding group, the rows of bony plates on the back would not exceed two.

Thus we should find that the second group held an exactly intermediate place between the first and third, and that the third set, in every respect in which it differed from the normal crocodilian structure, approached to that of lizards.

It is a very interesting point to see how these three groups appear in time. We should find that in the first are included all the Recent and Tertiary forms, and that there are no indications of the type below the later Cretaceous.

The second group would be found to extend from the older Cretaceous down to the Lias; moreover, a careful examination would show that there were lesser modifications among the individual species of a very instructive nature; those from the Wealden, for instance, would be seen to have the posterior nares farther back (*i.e.*, nearer the typical crocodilian position) than those of the middle Mesozoic, and these again than those of the Lias.

The third group would contain exclusively Triassic forms, such as the dragon-like *Belodon* and the *Stagonolepis* of the Elgin sandstones. In this latter formation the fossils are in a very curious condition; after the sand accumulated round the bodies of the Triassic animals had hardened, water, percolating through the porous rock, completely dissolved out the bones, leaving nothing but cavities. Thus we have only the remains of remains to deal with, but casts taken from the cavities enable us to make out, with perfect certainty, even important characters, although there may be hardly a bone left.

We see then, that our third set of forms is the oldest, our first

the youngest, and the study of crocodilian remains seem to show that that has happened in the history of crocodiles, which should have happened, if the theory of evolution be true. Anatomical characters show that crocodiles are a modification of the lacertian type, and to this type the Triassic species, from which we are certainly justified in supposing that existing forms are descended, exhibit a marked approximation.

Still we are very far from knowing the whole story: it is certainly allowable to assume that our third group of crocodilian forms was evolved from a common stock with lizards, but this is as far as the facts of the case will take us at present.

There seems, at first sight, to be something unnatural in speaking of birds and reptiles together, for no two animals can be, to all appearance, more unlike. The wonderfully constructed feathers of the one group, compared with the scutes and scales of the other, the cold blood of the reptile contrasted with the hot fluid which circulates through the vessels of a bird and raises its body several degrees above our own in temperature; the dumbness and general sluggishness of the reptile as compared with the vocal powers and the rapid flight of birds; all these compel us to say, and justly so, that nothing can be more different than the character of the two classes.

Even when we go more into details, similar differences are apparent. The bird has a small head, set on a long flexible neck, and provided with a horny beak in lieu of teeth; its bones are hollow and full of air; its breastbone, instead of being a small plate of cartilage, is a huge bony plate, usually provided with a large keel for the attachment of the powerful muscles of flight; the fore-limb is of no use in progression on the ground, and, the body having to be supported entirely by the hind limbs, the femora are placed parallel to the long axis of the body, instead of almost at right angles to it as in a reptile, so that the body is well raised from the ground, and a gait the very opposite of a reptile's sprawling waddle is the result.

The scapula and coracoid are not so very different from the corresponding bones in the lower class; the humerus, ulna, and radius, can also be perfectly well identified, but the modification of the distal division of the limb—the part answering to the reptile's fore-paw or to our own hand—is very great. First come two small bones answering to carpals, then three longer ones all united together, which represent the metacarpus, and are followed by the rudiments of the phalanges of the three corresponding digits. In the ostrich two of these three "fingers" are terminated by claws, the use of which it is rather hard to divine, unless the bird uses

them for scratching itself, an operation in which a very large portion of the activity of the lower animals is taken up.

The haunch-bone, or ilium, is of enormous size, and extends a long way in front of, as well as behind, the acetabulum; in correspondence with this, a great number of vertebræ are fused together to form a sacrum of sufficient size for the attachment of the ilia and the support of the weight of the body. The ischium and pubis are long slender bones, and the latter, as well as the former, is bent back, so that they both come to lie nearly parallel with the vertebral column.

To allow of the femur taking up its position parallel with the axis of the body, its well-finished globular head is set on at right-angles to the shaft; moreover, its further end has a characteristic notch for the reception of the upper extremity of the fibula. The shin-bone is provided with a large and very characteristic crest for the attachment of the strong muscles of the anterior part of the thigh; its lower extremity is pulley-shaped, and, in a young bird, the pulley-like end continued into a tongue of bone running up the back of the tibia, can be separated as a perfectly distinct ossification; its shaft also is so twisted that its two ends come to lie in different planes.

Following upon the tibia comes a bone with an easily separable piece at its upper end, and showing signs of a longitudinal division into three separate bones; this is the tarso-metatarsus, and represents the metatarsals and all the tarsals except one—the astragalus—which is represented by the pulley of the tibia. As a rule there are four toes, three of which are turned forwards and articulate with the tarso-metatarsus, while the fourth, the representative of our hallux or great toe, is turned backwards and articulates with a small distinct bone.

The heart has four perfectly distinct chambers, so that the pure blood from the lungs, and the impure blood from the rest of the body, are kept quite separate. There is a single aorta which turns to the right side after leaving the heart.

V[1]

We saw in the last lecture that the differences between birds and reptiles were very great; nevertheless, many of them tend to disappear on a closer examination. For instance, the extremely avian character of the absence of teeth, and the presence of a horny beak, is found in turtles and tortoises; that of the penetration of the bones by air cavities exists in the skull of crocodiles; and, although

[1] Delivered March 27, 1876.

no existing reptile possesses the power of flight, or a forelimb in any way approaching in structure to a bird's wing, yet, in the crocodiles, the fourth and fifth digits—those we found to be wholly absent in the bird—are much smaller than the others, and have no claws.

On passing to the internal organs, and the mode of development, we find far greater points of resemblance ; as to the latter, in fact, the correspondence is wonderful, the account given of the development of a reptile,[1] applying in every respect to that of a bird.

On the whole it is certain, from anatomical characters alone, that birds are modifications of the same type as that on which reptiles are formed, and if this similarity of structure is the result of community of descent, we should expect to find, in the older formations, birds more like reptiles than any existing bird, and reptiles more like birds than any existing reptile. If the Geological record were sufficiently extensive, and the conditions of preservation favourable, we ought to find an exact series of links, but this, of course, is hardly to be expected, and it will be a great step if we can show that certain forms tend to bridge over the gulf between the two groups.

Let us see, then, what the facts of Palæontology tell us in this matter : and first, as to birds.

It is a curious fact that, just as in the case of Crocodiles, all the birds found in the Tertiary deposits differ in no essential respects from those of the present day. Great numbers of remains have been found in beds of Miocene age—beds found at the bottoms of great lakes—and the very perfectly preserved specimens show, beyond any doubt, that the Miocene birds are referable to precisely the same groups as those of our own time. Our knowledge of the Eocene forms is less perfect, but enough is known to show that the same fact held good at the commencement of the Tertiary epoch.

Throughout the secondary period remains of birds are very rare ; until lately, in fact, there were none at all. But within the last ten or fifteen years some remarkable discoveries have been made—one or two in Europe, and a whole series in America, which give us some very precise information as to the nature of the Mesozoic birds.

Two of the most interesting of these—the genera *Hesperornis* and *Ichthyornis*—occur in certain beds in the United States, corresponding in age to our later Cretaceous. Hesperornis is stated, by its describer, to have had nearly the organisation of our Northern Diver (*Colymbus*) ; it was five or six feet in length, of swimming habits, had small wings, like those of the Penguin or Auk, and a long beak like

[1] *Nature*, vol. xiii. p. 429.

the Diver. But—and this is the interesting feature in its organisation—both jaws were beset with teeth: not mere serrations of the jaw, such as many existing birds have, but true teeth like those of a reptile. Here then we have the appearance of a true reptilian character.

Ichthyornis was, in some respects, even more curious. It was about as large as a good-sized pigeon, had large wings adapted for powerful flight, and teeth in both jaws, like Hesperornis. In another character it showed a still greater approximation to the lower reptilian type: the bodies of its vertebræ, instead of having the cylindroidal or saddle-shaped form so characteristic of nearly all birds,[1] were bi-concave. Thus, in tracing birds back in time, we find a parallel series of modifications to those described in the Crocodilia.

Beyond this point, the history of birds is almost a blank, the only other remains being—curiously enough—one or two feathers, and the *Archæopteryx* of the Solenhofen slates, a formation which has been of great service in the preservation of organic remains, the same qualities which make it so useful for purposes of lithography having fitted it for the preservation of even such perishable structures as jelly-fish.

Archæopteryx, known only by a single specimen now in the British Museum, was a bird about the size of a crow. Its head is unfortunately wanting; its tail is quite unlike that of any existing bird, being long, composed of a great number of vertebræ, and having two rows of feathers attached, one to each side of it. The leg is quite like that of any ordinary perching bird. Unluckily, the bones of the wing are detached, so that the exact structure of the manus is not known, but it is quite certain that the metacarpal bones were not united together, but were separate and terminated by distinct claws; there was thus an approximation in structure to a true forepaw. Long quills were attached to the wings, and both they and the tail-feathers are in an exquisite state of preservation.

With Archæopteryx we come to the end of all precise information as to the history of birds, and the only possible trace of the group in earlier formations are certain footprints found in the Trias of Connecticut, and referred to the genus *Brontozoum*. These were prints of some gigantic three-toed animal, which certainly walked on its hind legs, and was always supposed to be an ostrich-like bird until some recent discoveries, presently to be mentioned, have shown that Brontozoum may have been a reptile.

[1] In this peculiarly avian form of vertebra, the front face of the centrum is convex from above downwards, and concave from side to side, the hinder face being concave from above downwards, and convex from side to side. The Penguins have the dorsal vertebræ opisthocœlous, *i.e.*, with a ball in front and a cup behind.

It would at first seem easy to show an equally striking approximation of reptiles to birds, for we have, throughout the greater part of the secondary rocks, and notably in the Solenhofen slates, remains of a group of reptiles known as *Pterodactyles*. These remarkable creatures had teeth set in distinct sockets, sometimes extending to the end of the long snout, sometimes stopping short, and having their place taken by a horny beak. The neck was long; the sacrum consisted of from three to six vertebræ; the tail was short in some, long in other genera. The breast-bone had a great keel, like that of a bird, the shoulder-girdle was also quite bird-like, as also were the humerus and the bones of the fore-arm. The manus, on the other hand, was quite different to anything found in birds; the first, second, and third digits were of the usual reptilian character and bore claws, but the fourth was immensely prolonged, produced downwards, and clawless. The pelvis was, in some respects, birdlike, in others quite peculiar: the hind-limb was reptilian.

It is certain that the Pterodactyles were animals of flight, and that there was a membrane, like a bat's wing, stretched between the fourth finger and the sides of the body; it is also certain that it was unable to walk, though it may have used its hind-limbs, as bats do, for hanging itself head downwards from branches.

Although these creatures are, in many respects, very bird-like, yet it can hardly be said that they give us any direct help, or that they connect reptiles and birds any more than bats connect birds and mammals. Their avian characters seem to have been purely adaptive, or produced in relation to their peculiar mode of life, and we must therefore try some other line of reptiles for the origin of birds.

In the rocks from the Trias to the later Cretaceous there are, in many places, abundant remains of a group of wholly extinct terrestrial reptiles known as *Dinosauria*. Most of these are of great size, the genus *Iguanodon*, for instance, must have attained a length of fully thirty feet. Our knowledge of most of them is imperfect, but many points of the greatest possible interest are perfectly well known.

Some genera have the snout turned downwards like a turtle's beak, and both it and the large lower jaw were unsheathed in horn. In some the vertebræ are slightly excavated on both faces, and are penetrated with air cavities. The shoulder-girdle consists of a long blade-bone and a short coracoid like that of many lizards. Of the fore-limb nothing is known for certain in the larger species. The sacrum is composed of as many as six vertebræ, which often take on

a remarkably birdlike character. More curious still, the ilium has a great forward process, and the ischium and pubis are both turned backwards, parallel with one another, so as to have almost exactly the same position as in birds. There can be no doubt about this most remarkable point now, as the parts have been found in place in the genus *Hypsilophodon*. The femur was evidently brought parallel to the long axis of the body, and it has the characteristic ridge between the places of articulation of the tibia and fibula. The tibia has a great crest on its front surface the fibula is quite small, and the flattened end of the tibia fits on to a pulley-shaped bone exactly like the ankylosed astragalus of a bird. The middle or third toe is the largest, and the outer and inner toes small; the metatarsals, although separate from one another, have their faces so modelled that they must have been quite incapable of movement. Substitute ankylosis for ligamentous union, and a bird's metatarsus is produced; in fact the whole structure of the Dinosaurian hind-limb is exactly that of an embryonic bird.

In the very remarkable genus *Compsognathus* of the Solenhofen slates, which is nearly allied to the Dinosauria, and included, with them, in the order, *Ornithoscelida*, the head is small, the neck extremely long, and the peculiarities of the hind-limb are entirely birdlike; it also seems that the tibia and astragalus were actually united. The fore-limb, moreover, was very small, and it is certain that Compsognathus must have walked on its hind-legs.

The question, then, naturally arises, did the gigantic Dinosauria, such as Iguanodon and Megalosaurus, have the same mode of progression? This seems, at first sight, hard to believe, but there is considerable reason for thinking that it may have been the case, for, in the case mentioned above of the great three-toed footprints of the Connecticut valley and others found in the Wealden formation, no impression of a fore-foot has ever been found; so that, even if we suppose that the impressions of the fore-feet were entirely obliterated, as the animal walked, by those of the hind-feet, the former must, at any rate, have been very small.

When we consider what a very strong piece of evidence this is, we are forced to the conclusion that the evolution of birds from reptiles, by some such process as these facts indicate, is by no means such a wild speculation as it might, from *à priori* considerations, have been supposed to be.

VI[1]

In the highest group of Vertebrates, the Mammalia, the perfection of animal structure is attained. It will hardly be necessary, indeed it will be impossible, in the time at our disposal, to give the general characters of the group, but our purpose will be answered as well by devoting a short time to considering the peculiarities of a single well-known animal, the evidence as to the origin of which approaches precision.

The horse is one of the most specialised and peculiar of animals, its whole structure being so modified as to make it the most perfect living locomotive engine which it is possible to imagine. The chief points in which its structure is modified to bring about this specialisation, and in which, therefore, it differs most markedly from other mammals, we must now consider.

In the skull the orbit is completely closed behind by bone, a character found only in the most modified mammals. The teeth have a very peculiar character. There are, first of all, in the front part of each jaw, six long curved incisors or cutting teeth, which present a singular dark mark on their biting surfaces, caused by the filling in of a deep groove on the crown of each tooth, by the substances on which the animal feeds. After the incisors, comes on both sides of each jaw a considerable toothless interval, or *diastema*, and then six large grinding teeth, or molars and premolars. In the young horse a small extra premolar is found to exist at the hinder end of the diastema, so that there are, in reality, seven grinders on each side above and below; furthermore, the male horse has a tusk-like tooth, or canine, in the front part of the diastema immediately following the last incisor. Thus, the horse has, on each side of each jaw, three incisors, one canine, and seven grinders, making a total of forty-four teeth.

The grinding surfaces of the molars and premolars are very curious. In the upper jaw, each tooth is marked by four crescentic elevations, concave externally, the inner pair having each a curious folded mass connected with it. These projecting marks are formed of dentine and enamel, and, consequently, wear away more slowly than the intervening portions of the tooth, which are composed of cement. The lower grinders are marked with two crescents and two accessory masses, but the crescents are convex externally, and, consequently, when the opposite teeth bite together, the elevations do not correspond at any point. In this way a very perfect grinding surface

[1] Delivered April 3rd, 1876.

is obtained. The teeth are of great length, and go on growing for a long time, only forming roots in old animals. All these points contribute to the perfection of the horse as a machine, by rendering the mastication of the food, and its consequent preparation for digestion in the stomach, as rapid and complete a process as possible.

It is, however, in the limbs that the most striking deviation from the typical mammalian structure is seen, the most singular modifications having taken place to produce a set of long, jointed levers, combining great strength with the utmost possible spring and lightness.

The humerus is a comparatively short bone inclined backwards: the radius is stout and strong, but the ulna seems to be reduced to its upper end—the olecranon or elbow; as a matter of fact, however, its distal end is left, fused to the radius, but the middle part has entirely disappeared: the carpus or wrist—the so-called "knee" of the horse—is followed by a long "cannon-bone"; attached to the sides of which are two small "splint-bones": the three together evidently represent the metacarpus, and it can be readily shown that the great cannon-bone is the metacarpal of the third finger, the splint-bones those of the second and fourth. The splint-bones taper away at their lower ends and have no phalanges attached to them, but the cannon-bone is followed by the usual three phalanges, the last of which, the "coffin-bone," is ensheathed by the great nail or hoof.

The femur, like the humerus, is a short bone, but is directed forwards; the tibia turns backwards, and has the upper end of the rudimentary fibula attached to its outer angle. The latter bone, like the ulna, has disappeared altogether as to its middle portion, and its distal end is firmly united to the tibia. The foot has the same structure as the corresponding part in the fore-limb—a great cannon-bone, the third metatarsal; two splints, the second and fourth; and the three phalanges of the third digit, the last of which bears a hoof.

Thus, in both fore and hind limb one toe is selected, becomes greatly modified and enlarged at the expense of the others, and forms a great lever, which, in combination with the levers constituted by the upper and middle divisions of the limb, forms a sort of double C-spring arrangement, and thus gives to the horse its wonderful galloping power.

In the river-beds of the Quaternary age—a time when England formed part of the Continent of Europe—abundant remains of horses are found, which horses resembled altogether our own species, or perhaps are still more nearly allied to the wild ass. The same is the case in America, where the species was very abundant in the

Quaternary epoch—a curious fact, as, when first discovered by Europeans, there was not a horse from one end of the vast continent to the other.

In the Pliocene and older Miocene, both of Europe and America, are found a number of horse-like animals, resembling the existing horse in the pattern and number of the teeth, but differing in other particulars, especially the structure of the limbs. They belong to the genera *Protohippus*, *Hipparion*, &c., and are the immediate predecessors of the Quaternary horses.

In these animals the bones of the fore-arm are essentially like those of the horse, but the ulna is stouter and larger, can be traced from one end to the other, and, although firmly united to the radius, was not ankylosed with it. The same is true, though to a less marked extent, of the fibula.

But the most curious change is to be found in the toes. The third toe, though still by far the largest, is proportionally smaller than in the horse, and each of the splint bones bears its own proper number of phalanges; a pair of "dew-claws," like those of the reindeer, being thus formed, one on either side of the great central toe. These accessory toes, however, by no means reached the ground, and could have been of no possible use, except in progression through marshes.

The teeth are quite like those of the existing horse, as to pattern, number, presence of cement, &c.; the orbit also is complete, but there is a curious depression on the face-bones, just beneath the orbit, a rudiment of which is, however, found in some of the older horses.

On passing to the older Miocene, we find an animal, known as *Anchitherium*, which bears, in many respects, a close resemblance to Hipparion, but is shorter-legged, stouter-bodied, and altogether more awkward in appearance. Its skull exhibits the depression mentioned as existing in Hipparion, but the orbit is incomplete behind, thus deviating from the specialised structure found in the horse, and approaching nearer to an ordinary typical mammal. The same is the case with the teeth, which are short and formed roots at an early period; their pattern also is simplified, although all the essential features are still retained. The valleys between the various ridges are not filled up with cement, and the little anterior premolar of the horse has become as large as the other grinders, so that the whole forty-four teeth of the typical mammalian dentition are well developed. The diastema is still present between the canines and the anterior grinding teeth—a curious fact in relation to the theory

that the corresponding space in the horse was specially constructed for the insertion of the bit ; for, if the Miocene men were in the habit of riding the Anchitherium, they were probably able to hold on so well with their hind legs as to be in no need of a bit.

The fibula is a complete bone, though still ankylosed below to the tibia ; the ulna also is far stouter and more distinct than in Hipparion. In both fore and hind foot the middle toe is smaller, in relation to the size of the animal, than in either the horse or the Hipparion, and the second and fourth toes, though still smaller than the third, are so large that they must have reached the ground in walking. Thus, it is only necessary for the second and fourth toes, and the ulna and fibula to get smaller and smaller for the limb of Anchitherium to be converted into that of Hipparion, and this again into that of the horse.

Up to the year 1870 this was all the evidence we had about the matter, except for the fact that a species of *Palæotherium* from the older Eocene was, in many respects, so horse-like, having, however, well-developed ulna and fibula, and the second and fourth toes larger even than in Anchitherium, that it had every appearance of being the original stock of the horse. But within the last six years some remarkable discoveries in central and western North America have brought to light forms which are, probably, nearer the direct line of descent than any we have hitherto known.

In the Eocene rocks of these localities, a horse-like animal has been found, with three toes, like those of Anchitherium, but having, in addition, a little style of bone on the outer side of the fore foot, evidently representing the fifth digit. This is the little *Orohippus*, the lowest member of the Equine series.

This evidence is conclusive as far as the fact of evolution is concerned, for it is preposterous to assume that each member of this perfect series of forms has been specially created ; and if it can be proved—as the facts adduced above certainly do prove—that a complicated animal like the horse may have arisen by gradual modification of a lower and less specialised form, there is surely no reason to think that other animals have arisen in a different way.

This case, moreover, is not isolated. Every new investigation into the Tertiary mammalian fauna brings fresh evidence, tending to show how the rhinoceros, the pigs, the ruminants, have come about. Similar light is being thrown on the origin of the carnivora, and also, in a less degree, on that of all the other groups of mammals.

It may well be asked why such clear evidence should be obtainable as to the origin of mammals, while in the case of many other groups—fish, for instance—all the evidence seems to point the other way. This

question cannot be satisfactorily answered at present, but the fact is probably connected with the great uniformity of conditions to which the lower animals are exposed, for it is invariably the case that the higher the position of any given animal in the scale of being, the more complex are the conditions acting on it.

It is not, however, to be expected that there should be, as yet, an answer to every difficulty, for we are only just beginning the study of biological facts from the evolutionary point of view. Still, when we look back twenty years to the publication of the 'Origin of Species,' we are filled with astonishment at the progress of our knowledge, and especially at the immense strides it has made in the region of palæontological research. The accurate information obtained in this department of science has put the *fact* of evolution beyond a doubt; formerly, the great reproach to the theory was, that no support was lent to it by the geological history of living things; now, whatever happens, the fact remains that the hypothesis is founded on the firm basis of palæontological evidence.

XIII

THE CROCODILIAN REMAINS FOUND IN THE ELGIN SANDSTONES, WITH REMARKS ON THE ICHNITES OF CUMMINGSTONE

Memoirs of the Geological Survey of the United Kingdom, Monograph III., 1877.

I.—STAGONOLEPIS ROBERTSONI.

I. Introductory Remarks upon the Discovery of Reptilian Remains in the Elgin Sandstones, and upon the Geological Age of those Sandstones.

At p. 139 of the late Professor Agassiz's celebrated "Poissons Fossiles du vieux Grès rouge," a passage occurs of which I give the following translation.

Genus *Stagonolepis*, Agass.

"I have established this genus upon a slab on which are observable the impressions of many series of great rhomboidal scales, disposed in the same manner as those of the *Lepidosteidæ*. The angular form of these impressions allows of no doubt that the fish whence they proceeded was a great Ganoid allied to *Megalichthys*. The absence of the fins, of the head, and of teeth, however, prevents the rigorous determination of the family to which this fossil belongs. I arrange it, provisionally, near the genus *Glyptopomus*, with which it has some analogy

in the ornamentation of its scales. However, this genus *Stagonolepis* cannot be confounded with any of those which I have hitherto established. The surface of its scales is adorned with hollows, having the shape of elongated drops, disposed like a rosette around the centre of each scale; these hollows increase in size towards the periphery, without, however, reaching the margins, which are smooth. I know as yet but a single species of this genus, the *Stagonolepis Robertsoni*, Ag., Old Red., Tab. 31, figs. 13 and 14.

"Figure 13 represents the impression of four scales, of the natural size and in their normal position. Figure 14 is a drawing of the entire specimen which was observed by Mr. Robertson, reduced to one half of the natural size. This fossil was obtained from the upper beds of the Old Red Sandstone of Morayshire. It was discovered in the neighbourhood of Elgin, at Lossiemouth. I have not examined the original myself, but the drawings which Mr. Robertson has communicated to me, and which I have reproduced in the plates of my Atlas cited above, are sufficient to enable me to recognise the type of an entirely new genus. In the fossil in question, the ornaments of the scales are in relief; but it must not be forgotten that it is only an impression and that, consequently, the scales, in their natural state, must have their ornamentation hollow."

Considering that when Professor Agassiz wrote, the Devonian age of the Elgin Sandstones was generally accepted, and keeping in mind the singular resemblance in arrangement and ornamentation which really obtains between the exoskeleton of *Stagonolepis* and that of *Glyptopomus*, an undoubtedly Devonian fish, there is nothing to excite surprise either in his determination of the nature of the fossil, or in the fact that Agassiz's interpretation was adopted, without hesitation, by geologists and zoologists. The late Sir Charles Lyell, however, informed me that, many years ago, after perusing Dr. A. Wagner's Memoir on *Mystriosaurus*, the strong resemblance between the sculpture of the dermal plates of *Stagonolepis* and that exhibited by the scales of *Mystriosaurus*, as figured by Wagner, excited his suspicions as to whether, after all, *Stagonolepis* might not be a reptile. But, on communicating these doubts to the late Mr. Hugh Miller, that experienced investigator of the fishes of the Old Red Sandstone expressed himself so unhesitatingly in favour of the piscine nature of *Stagonolepis* that Sir Charles Lyell's scruples were satisfied, and it was not until the year 1858 that the question, whether *Stagonolepis* was really a fish, was revived.

In that year, however, the late Sir Roderick Murchison, the then Director General of the Geological Survey of the United Kingdom,

was engaged in those remarkable investigations of the structure of the Highlands of Scotland which led to a complete change in the views which geologists had, up to that time, entertained on the subject.

In the course of his inquiries, Sir Roderick Murchison was led to visit Elgin and its neighbourhood, and to inspect the fossils of the district contained in the Elgin Museum and in the private collections of the late Mr. Patrick Duff and the Reverend Dr. George Gordon. Among these was the original specimen of *Stagonolepis Robertsoni* (Plate I. [Plate 8] fig. 1), a cast in sandstone of the ornamented dermal plates of an animal which Agassiz had every reason to think might be a fish, and of which, it must be recollected, he saw only a drawing transmitted to him by Dr. Robertson. But, subsequently to the publication of Agassiz's observations upon *Stagonolepis*, additional specimens had been obtained, in which, associated with the *Stagonolepis* scutes in such a manner that there could be no doubt that they belonged to the same animal, were fragments or casts of bones of so obviously reptilian a character as to awaken grave doubts in the mind of their discoverer, the Rev. Dr. Gordon, as to the nature of the supposed fish, and to lead him to believe that *Stagonolepis* must be an animal of higher organization.

Apart from the interest of the purely zoological question thus raised, the existence of any vertebrated animal of higher grade than a fish in the sandstones of Findrassie and Lossiemouth was a fact of great geological importance. The Elgin district had yielded a small quadrupedal vertebrated animal, the *Telerpeton Elginense* of Mantell (the amphibian or reptilian nature of which was still a matter of dispute), and, in addition, many footmarks of very much larger quadrupedal *Vertebrata*. So that there was nothing unexpected in the discovery of the actual bones and scutes of such animals. But the discussion respecting the age of the Elgin sandstones, which had been awakened by the discovery of the footprints and of *Telerpeton*, had ended in the general admission that they belonged to the Devonian epoch; and this conclusion was confirmed by Sir R. Murchison's renewed study of the district.

It appeared, therefore, that the remains of *Stagonolepis* were calculated to throw a new light upon the vertebrate Fauna of the Devonian epoch; and Sir R. Murchison used every effort to bring together all the materials which could be of service. In these efforts Sir Roderick Murchison was aided in the most zealous and liberal manner by the committee of management of the Elgin Museum, by the late Mr. Patrick Duff, and by the Rev. Dr. Gordon.

One or two of the fossils thus obtained were exhibited by Sir

Roderick Murchison at the meeting of the British Association at Leeds in 1858, but no person who examined them expressed a more definite opinion than that at which Sir Roderick himself had arrived, namely, that they were reptilian in their general character. On his return to London in the autumn of 1858, the Director General informed me of what he had seen at Elgin, and told me that Sir Philip Egerton and Professor Owen, who had cursorily examined the fossils exhibited at Leeds, had as little doubt respecting their reptilian nature as himself. But no one had expressed any opinion as to the group of reptiles to which *Stagonolepis* belonged, and Sir Roderick desired that I should undertake the investigation of the problem. To this end the fossils which had been exhibited at Leeds were placed at my disposal; while the larger and more important series which had remained at Elgin were sent direct to me. It was on these materials that I based the conclusion that *Stagonolepis* is a crocodilian reptile; a fact of which Sir R. Murchison had no suspicion when he placed the inquiry in my hands and the announcement of which caused him the liveliest surprise, believing as he did that the Elgin beds were of Devonian age. Moreover, I found that all the Elgin fossils did not belong to the same genus; but that, in addition to *Telerpeton*, there was at least one other reptile, which I named *Hyperodapedon Gordoni*.[1]

In 1859, I had the opportunity of examining the collection of Dr. Taylor, and the series of Elgin fossils contained in the Museum of Aberdeen. And, since that time, the Rev. Dr. Gordon, to whose help I am very greatly indebted, has kept me informed of all the discoveries of fossils in the quarries of the neighbourhood which have come to his knowledge; and, aided by a grant from the donation fund of the Royal Society, has made explorations which have yielded most valuable results. Mr. Grant, of the Schoolhouse, Lossiemouth, has further helped by the loan of specimens, and I have thus been enabled to add from time to time to what was known respecting *Hyperodapedon* and *Telerpeton*.[2] But it is a singular fact that, in the course of the nineteen years during which the produce of the quarries about Elgin has been carefully scrutinized, the only remains which have been discovered are those of *Stagonolepis*, *Hyperodapedon*, *Telerpeton*, and the jaw with large teeth described in my first paper, and which I then ascribed to *Stagonolepis*; though the subsequent discovery of the true teeth of *Stagonolepis* enables me to correct that error.

[1] See my paper "On the *Stagonolepis Robertsoni* (Agassiz) of the Elgin Sandstones, and on the recently discovered Footmarks in the Sandstones of Cummingstone," read before the Geological Society, December 15th, 1858.

[2] "On a new specimen of *Telerpeton Elginense*," 'Quarterly Journal of the Geological Society,' 1866.

In the brief notice of *Hyperodapedon*, appended to my paper of 1858, I said that "its marked affinity with certain Triassic reptiles, "when taken together with the resemblance of *Stagonolepis* to "Mesozoic *Crocodilia*, leads me to require the strongest stratigraphical "proof before admitting the Palæozoic age of the beds in which it "occurs." And Sir R. Murchison, even then, admitted that his belief in the Devonian age of the Elgin sandstones was somewhat shaken by the discovery of the true nature and affinities of these reptilian remains.

In fact, this discovery led to a re-investigation of the age of the Elgin sandstones by several eminent geologists, among others, the late Sir Charles Lyell, with the result that opinions and weight of authority were about equally divided; Murchison, Ramsay, Harkness, and others, being inclined still to regard them as Palæozoic, while Lyell and Moore advocated the view that they were Triassic.

In the years 1866, 1867, and 1868, however, some remarkable facts came to light, which brought the question into a new phase. Remains of *Hyperodapedon* were proved to occur in the unquestionable Trias of Coton-End in Warwickshire, and in beds of Triassic age in Devonshire; while, in Central India, jaws of a large species of *Hyperodapedon* were found, in association with Labyrinthodonts and *Crocodilia*, at Maledi, in beds to which, on independent grounds, a Triassic or Permian age had been assigned.[1]

In view of these facts, Sir Roderick Murchison remarks at p. 267 of the fourth edition of "Siluria" published in 1867:

"To such fossil evidence as this the field geologist must bow; and instead, therefore, of any longer connecting these reptiliferous sandstones of Elgin and Ross with the Old Red Sandstones beneath them, I willingly adopt the view established by such fossil evidence, and consider that these overlying sandstones and limestones are of Upper Triassic age."

II. Description of the Remains of Stagonolepis Robertsoni. (Plates I. to VIII. [Plates 8–15].)

The fossils, which may be safely referred to *Stagonolepis Robertsoni*, which have come into my hands, afford a tolerably complete view of the whole bony structure of the animal, and consist of—

1. Dermal scutes.
2. Vertebræ from all parts of the vertebral column and ribs.
3. Portions of the skull with teeth.
4. Bones belonging to the pectoral and pelvic arches, and to the respective limbs.

[1] "On *Hyperodapedon*," 'Quarterly Journal of the Geological Society,' 1869.

In the soft sandstones of Lossiemouth, the actual substance of the bones and teeth is preserved, though in an exceedingly soft and friable state. In the more firmly grained and harder sandstones of Findrassie, on the other hand, nothing but casts remain, though these are sometimes so perfect as to retain the outward form of their originals with great fidelity.

Portions of at fewest three, and probably of many more, individuals have been met with. In the largest of these, the bones were about twice the size of those of a *Crocodilus biporcatus*, 7 feet long, whence I conclude that this *Stagonolepis* measured 12 or 14 feet in length. The smallest had about two-thirds of the dimensions of the largest.

1. *The Dermal Scutes of Stagonolepis Robertsoni.* (Plates I., II., III., IV. [Plates 8, 9, 10, 11].)

The remains referable to this part of the organization of *Stagonolepis* consist of stout broad plates of bone, or their casts. These scutes are primarily distinguishable into two kinds, the *flat* and the *angulated;* the former being distinguished by their flattened inner and outer surfaces, and their nearly square shape; while the latter present a more or less elevated longitudinal ridge on their outer surface, to which an excavation of the inner surface corresponds.

The flat Scutes of Stagonolepis.—The sandstone cast upon which the *Stagonolepis* was originally founded exhibits a very characteristic impression of a considerable number of these scutes with their natural relations almost undisturbed. The sculptured portion of this specimen is represented of the natural size in Plate I. [Plate 8] fig. 1, and a reproduction of the sculpture on the outer surface of two of the original scutes, effected by taking a plaster-cast from it, is given in fig. 1a of the same Plate.

The specimen is an irregularly broken mass of sandstone, the convexo-concave face of which exhibits numerous impressions of four-sided scutes. Of these there are, altogether, five rows in one direction and eleven, with a fragment of a twelfth, in the other. A plaster-cast shows, even better than the original, that, while one opposed pair, out of the four edges of each scute, fitted against the adjoining edges of the scutes on each side, the other pair of edges alternately overlapped, and were overlapped by, those of the adjacent scutes. There can be no doubt that the overlapped edges were anterior, and, as I shall presently show, that these scutes formed part of the ventral armour of the animal to which they belonged, the direction and relations of each row become at once definable. The five rows are longitudinal—

the eleven transverse. None of these rows are complete. The left-hand longitudinal row contains five scutes, whose outer edges are more or less broken away. The next row contains seven scutes, the posterior of which are somewhat thrust forward, and their left edges somewhat broken. The third row contains eight scutes and the right sides of the anterior four are defective. Each of these longitudinal rows extends to the same level anteriorly; but the next, or fourth, series begins opposite the fifth scute of the third series, and but a very small portion of its most anterior scute is visible. This is followed by six scutes, of which the hindermost are somewhat displaced and thrown forwards one upon the other. The fifth series contains only the impressions of the halves of five scutes. The impression of an additional small fragment of a scute is visible in front of the first and third series.

Each scute is on exactly the same level as its right-hand and left-hand neighbour, so that the structure of the whole fragment is extremely regular. About a fifth of the outer surface of each scute is covered by the posterior edge of its predecessor; and the fifth and sixth scutes of the fourth series are sufficiently displaced to show that the covered surface was smooth and bevelled off obliquely, and thus constituted a sort of articular facet, narrow and parallel-sided antero-posteriorly, but very wide transversely.

The posterior edge of this facet is cut perpendicularly to the plane of the scute, from the face of which it rises like a kind of parapet. The face of the scute was ornamented with a peculiar sculpture, consisting of distinct deep pits. The casts of these are of course elevated, and lie like drops upon the general surface of the impression—an appearance which doubtless suggested the name of the genus. Near the centre of the face of the scute, the pits are nearly circular in outline, but, towards the periphery, they elongate in the direction of radii from a point rather nearer the anterior than the posterior edge of the whole scute, and assume a pyriform shape, the small end of each being directed inwards. The consequence of this arrangement is a very marked radiation of the ornamentation from a centre which lies about the junction of the anterior two-fifths with the posterior three-fifths of the whole ornamented surface. A small marginal space, laterally and posteriorly, is, as Agassiz has observed, free from sculpture.

An inch and a quarter transversely, by a little less antero-posteriorly, is a fair statement of the average dimensions of these flat scutes.

Very many examples of the actual scutes, of which the fossil just described presents only the impressions, have been discovered in the

Lossiemouth sandstones. A specimen in the collection of Dr. Taylor of Elgin exhibits five longitudinal series of flat scutes, but very little disturbed from their natural relations. The most complete of these longitudinal series contained eight scutes and occupied a length of about 7 inches. They gradually increase in size from one end of the series to the other, the smallest being rather less than 1·0 inch square, and the largest 1·0 inch long by 1·4 inch wide.

Two of the most perfect of these scutes are represented of the natural size in Plate I. [Plate 8] fig. 2.

Each exhibits, along the whole width of its anterior side, a smooth facet, obliquely bevelled off to the free edge and measuring about 0·2 inch in its narrow or antero-posterior diameter. Behind this articular facet is a well-marked, but shallow, transverse groove, which separates the smooth facet from the sculptured portion of the scute. The sculpturing consists of shallow rounded or elongated pits, which radiate from a common centre; it is, in fact, the exact converse of the sculpturing in the cast. In some parts of the cast, the facet on a scute is still overlapped by the free posterior edge of the scute in front, and the direction of the articular facets shows that the narrow end of each longitudinal series was the anterior, the broad end posterior. Traces of what appeared to be ribs are visible amongst the impressions of the scutes at one end of the fossil; and, on the opposite or under side of the block to that which shows the flat scutes which have been described, there are many, much crushed, flat scutes having their faces turned in the same way as those of the upper side. Sections of scattered dorsal scutes are visible in the thickness of the block.

The most complete set of flat scutes, however, is presented by a slab of Lossiemouth sandstone in the Museum of Aberdeen University, which shows the remains of seven longitudinal rows of such scutes. The smooth deep surfaces of all these are turned to the eye, but, on clearing away the osseous substance of one, the characteristic sculpture of the exterior appeared in relief on the matrix. There are indications of ten transverse rows of scutes. Four scutes in each row are of equal sizes, and, in all but the hindermost rows, are of a rectangular quadrilateral figure; they measure 1·4 inch anteposteriorly and 2·1 inches transversely. The scutes in the hindermost rows have their angles rounded off and are small, but it is difficult to ascertain their exact dimensions. On the left side two scutes lie, in each transverse row, at one end of the series of four rectangular ones. The inner of these is nearly as large as one of the latter, but not quite so wide, and its outer margin is either oblique or rounded: the outermost scute, although it has the same length as the inner, is much narrower, and its

representative appears to have been wanting in the hindermost two or three rows. On the right side the remains of only a few of the scutes which answer to the inner of these smaller scutes are present.

The relative sizes and the arrangement of the scutes in these specimens lead me to conclude that there were six principal flat scutes in each transverse series; but that, in some rows, a smaller and less regular scute was added upon each side, making eight in all.

On comparing these scutes with those which constitute the ventral armour of a *Teleosaurus* (Plate XI. [Plate 18]), or of an existing *Jacare* (Plate I. [Plate 8] fig. 3), or *Caiman* (Plate XIII. [Plate 20]), there can be no doubt as to their being structures of the same order.

But, apart from the general grounds for arriving at this determination, there is direct evidence that the flat scutes were disposed upon the ventral region of the body of *Stagonolepis*. Such evidence is afforded by one of the most singular fossils which has ever come under my notice, and which is, in fact, the natural cast, in sandstone, of the anterior caudal scutes and vertebræ of a *Stagonolepis*, but little disturbed from their natural position. This fossil, which is represented of three-fifths the natural size in Plate III. [Plate 10] figs. 1, 1a, 1b, was discovered by Mr. Patrick Duff, who caused it to be sawn through longitudinally. A view of the cut face of one half is exhibited in Plate III. [Plate 10] fig. 1c, and it is at once seen to exhibit a series of hourglass-shaped cavities, separated from one another by sandstone partitions, and to be traversed above two of these cavities by bars of sandstone attached at each end to these sandstone partitions, but quite free at the sides, and thicker in the middle than at each end. It was at once obvious that the hourglass-shaped cavities in question were the impressions of the centres, while the sandstone bars were the casts of the neural canals of vertebræ; but, in order to study the characters of these vertebræ more conveniently, I caused casts to be taken of the different parts of the fossil,[1] and these reproductions of the original specimen are represented in Plate III. [Plate 10] fig. 2, and Plate IV. [Plate 11] figs. 3 and 4. Plate IV. [Plate 11] fig. 4, is a cast of the anterior of the left half of the fossil, or that represented in Plate III. [Plate 10] fig. 1c. Plate III. [Plate 10] fig. 2, represents a cast of the interior of the right half, and Plate IV. [Plate 11] fig. 3, a cast of the surface of the fossil represented in Plate III. [Plate 10] fig. 1.[2]

I shall have to revert to the peculiarities of the vertebræ reproduced in these casts at a future page; at present I merely wish to

[1] These were made with great skill by Mr. Brucciani.

[2] The drawings have not been reversed by the artist.

point out that they are obviously very little disturbed from their natural position, the majority of them being still articulated together, and their form and size being such that it is impossible they should have become exactly reversed within the dermal plates without dislocation. But if the vertebræ are not thrown out of their natural position, it follows that the dermal plates, the casts of which lie immediately under their centra, were ventral scutes.

Now these casts show (Plate IV. [Plate 11] fig. 3) that the scutes in question were flat quadrilateral bony plates, with nearly straight edges, quite smooth upon their internal or upper faces, and sculptured, like those already described, upon their external or under faces.

The largest of these scutes has left an impression about 2·4 inches wide by nearly 2 inches long. The entire width of the fossil, at this point, is a little more than 4½ inches ; hence, the ventral surface of the tail must have been covered by not more than two scutes.

Immediately behind this part, the fossil suddenly narrows, and at the same time, the cast shows that this results from the displacement of one series of ventral scutes which, having at first been driven inwards, have then been thrown into a perpendicular position, the scutes of the other series remaining nearly horizontal. As these measure fully 2 inches in width and about 1·7 inch antero-posteriorly, and as there must have been at least two scutes in a transverse row, it follows that the apparent sudden narrowing of the tail simply arises from post-mortem distortion ; and that it must, in reality, have tapered to but a very slight extent in the length of 10 inches, which is the longitudinal dimension of the specimen.

Altogether the casts of six transverse rows of ventral scutes appear.

The dorsal face of the specimen differs widely from the ventral. It is, in fact, strongly convex ; so that, in transverse section, the fossil would have the contour of a high arched window, the ventral scutes representing the sill, and the dorsal, the arch of the window. Strong transverse ridges mark this aspect of the fossil and divide it into eight segments, of which the first and the last are very short. Each of the segments corresponds with the inner face of a large dermal plate, and every plate must have been so bent upon itself that its internal face was strongly concave from side to side, and slightly convex from before backwards, inasmuch as the faces of the cast present the converse contours in these directions. Furthermore, at some points, the posterior plate must have slipped forwards and inwards under that which preceded it, for the backwardly projecting ridges of the natural cast are formed by the sandstone, which has

been, as it were, run in between the displaced posterior edge of the one plate and the anterior edge of the next. The cavity underneath each ridge should therefore give the form of the anterior edge of one of these plates; and, on examination, it shows that like the ventral scutes, the dorsal plates were terminated by a bevelled-off anterior articular facet. The analogy of *Teleosaurus* (Plate XII., [Plate 19] fig. 1*c*) and of *Caiman* (Plate XIII. [Plate 20] fig. 1) leads to the suspicion that each dorsal plate of the tail was composed of two scutes united by suture in the median line; and though the impression of the inner edges of the scutes of each side are not very distinctly traceable, sufficient remains to show that there really were two distinct series. The outer edges of the scutes were truncated and rather produced at their anterior angles. In fact, the general form of each dorsal scute would be represented by a broad parallelogram of bone, bent upon itself along a longitudinal line drawn nearer the inner than the outer margin.

The anterior dorsal plates of this fragment of the tail are larger than the posterior ones; the most anterior measuring not less than 3½ inches transversely, by two inches antero-posteriorly. The three anterior ones correspond very nearly with the three anterior zones of ventral scutes; but while, in the fourth zone, the ventral scutes are displaced a little backwards, the dorsal plates have slipped forwards; whereby the posterior edges of the dorsal scutes nearly correspond with the middle of the ventral scutes. This displacement is continued in the succeeding zones, whence the greater number of dorsal than of ventral scutes.

The angulated scutes of Stagonolepis.—Although this interesting specimen affords complete information as to the general form of the inner surfaces of the dorsal scutes, it tells nothing of the appearance of their external surfaces, the sandstone mould of the exterior of the scutes, in which the specimen doubtless lay loose, not having been preserved. But a considerable series of scutes and their casts have been obtained, all of which are bent or angulated in the same way as though, usually, to a less extent than, the dorsal scutes of the caudal fragment; and partly on this ground, and partly by analogical reasoning, from the characters commonly presented by the dorsal scutes of crocodilian reptiles (Plate XIII. [Plate 20] fig. 1. and 1e) I have no hesitation in referring these *angulated* scutes to the dorsal region of the body of *Stagonolepis*.

Various examples of such scutes are represented in Plate II. [Plate 9]. Two chief forms are readily distinguishable; the one much broader than they are long (Plate II. [Plate 9] figs. 1, 2, 3, 10, 11); the

others (Plate II. [Plate 9] figs. 4, 5, 6) longer than broad; but, occasionally, scutes are met with (Plate II. [Plate 9] figs. 7, 8, 9) which are transitional in form between these two extremes, and then are remarkably thick. In the *broad angulated scutes* the antero-posterior diameter of the scute may be less than half its transverse diameter (Plate II. [Plate 9] fig. 2), but, in some, the two dimensions approach equality. The anterior edge (directed downwards in all the figures) is straight or slightly concave forwards. The posterior edge may be straight or sinuous, or produced in correspondence with the ridge on the outer face. The median edge is straight and cuts the line of the anterior edge at a right angle. The lateral edge is curved or sloping with the postero-lateral angle rounded off. The ventral surface is smooth and concave from side to side, the deepest part of the concavity forming a longitudinal depression which is situated nearer the median than the lateral edge of the scute. In correspondence with this, the dorsal surface of the scute presents a more or less marked ridge, which not unfrequently runs out posteriorly into a projecting spine. The scute is thickest in the region occupied by this ridge, and especially in its posterior part. Immediately behind the whole length of the anterior margin, the dorsal face presents a narrow smooth surface by which the scute articulated with that which preceded it. The rest of this dorsal face is ornamented by a series of depressions which radiate from the ridge, and have the form of pits close to the ridge, while they become elongated grooves further away from it. It is obvious from the form of these scutes that, like the more strongly bent scutes in the caudal region, they formed a double series along the middle line of the back, each scute being articulated by its median edge to one of corresponding form and size upon the opposite side of the median line; while the pair thus formed overlapped the pair which succeeded them, and were overlapped by the pair which preceded them.

The largest specimens of dorsal scutes I have met with do not exceed five inches and a half in transverse, and two inches and a half in antero-posterior, diameter.

Stagonolepis, therefore, possesses a dorsal shield composed of dermal ossifications, and consisting of two longitudinal series of angulated scutes arranged in pairs, each pair articulating with the pair in front of and behind it. In the caudal region of the body, the scutes of the dorsal shield are greatly bent, so as to roof over the top and sides of the tail, and their lateral edges probably unite with those of the ventral shield as they do in recent *Jacares* and *Caimans* (Plate XIII. [Plate 20] fig. 1b. The lateral edges of the scutes of the dorsal

shield in the rest of the body, on the other hand, are free; and, as in those existing *Crocodilia* which possess a ventral armour, were united with the ventral shield only by the integument. These scutes are less bent, and may be nearly flat, but always present a ridge, which often ends behind in a point. *Stagonolepis* also possesses a ventral shield made up of similar dermal ossifications, which were flat and devoid of any ridge. These scutes are rectangular and are disposed in longitudinal rows, of which only two appear to exist in the tail, while there are probably six, or in some parts eight, in the thoraco-abdominal region. Each ventral scute has an anterior smooth facet, and is overlapped by and overlaps its predecessor and successor, as in the dorsal shield; and the straight median and lateral edges of each scute are suturally united with those of adjacent scutes, except in the case of the lateral edges of those scutes which formed the lateral series on each side. Thus, in the thoraco-abdominal region, the ventral armour forms a series of flat and wide bands, each made up of six or eight firmly united pieces, and overlapping the band which follows it; while, in the same region, the dorsal armour is composed of less wide, ridged bands, each made up of only two pieces.

The *narrow angulated scutes* exhibit no articular surfaces or straight edges for union with other scutes. They probably were situated in the integument, between the dorsal and ventral shields and on the limbs, as in recent *Crocodilia.* (Plate XIII. [Plate 20] fig. 1d.)

As is the case with the dorsal scutes, each ventral scute is composed, so far as I have been able to observe, of only one piece of bone, the anterior part of the scute, which bears the articular facet, not being separated from the rest by a suture. In this respect they differ from the ventral scutes of *Jacare* (Plate I. [Plate 8] fig. 3) and of *Caiman*, (Plate XIII. [Plate 20] fig. 1f.)

2. *The Vertebræ and the Ribs of Stagonolepis Robertsoni* (Plates I., III., IV., V., VII., VIII., X. [Plates 10, 11, 12, 14, 15, 17]).

The atlas and axis have not yet been discovered; but I have other cervical vertebræ and vertebræ from the thoracic, sacral and caudal regions. In all these vertebræ, the articular facets at the anterior and posterior ends of the centra are slightly concave. The cervical vertebræ (Plate I. [Plate 8] figs. 6 and 7) have the contours of these facets nearly as broad as they are high, and the centra themselves are short and but little contracted in the middle.

In the thoracic vertebræ (Plate I. [Plate 8] fig. 5; Plate V.

[Plate 12] figs. 2 and 3; Plate VII. [Plate 14] fig. 2,) the contours of the articular faces of the centra are oval, the vertical being greater than the transverse diameter; the centra themselves are elongated and much narrower in the middle than at the ends.

In the sacral vertebræ (Plate V. [Plate 12] figs. 4, 4a, Plate X. [Plate 17], fig. 10), the articular faces of the centra are broader than they are high; while, in the caudal region (Plates III., IV. [Plates 10, 11], figs. 2 and 4, VII. [Plate 14] figs. 1 and 4) they nearly return to the form of those of the thoracic vertebræ.

In some of the vertebræ both of the thoracic and caudal regions, the articular faces of the centra of the vertebræ are not disposed at right angles to the axis of the centrum, but have a slight inclination from above downwards and backwards (Plate V. [Plate 12] fig. 2; Plate III. [Plate 10] fig. 2). In the thoracic region, the spines of the vertebræ are stout and broad from before backwards, but not very high (Plate VII. [Plate 14] fig. 2). They are lower in the anterior part of the tail (Plate IV. [Plate 11] fig. 2; (Plate VII. [Plate 14] fig. 1), and disappear altogether in the posterior part of this region (Plate VII. [Plate 14] fig. 4). These, like the other processes of the vertebræ, are altogether similar in their general characters to those of existing *Crocodilia*, but the thoracic vertebræ are remarkable for the very strong upward inclination of their transverse processes. Living *Crocodilia* vary in the degree in which this bending upward of the transverse processes of the thoracic vertebræ takes place, but in none that I have met with is the inclination so great as in *Stagonolepis*.

The fragmentary cast of part of a sacral vertebra, from Findrassie, represented in Plate V. [Plate 12] figs. 4, 4a, was among the earliest of the specimens which came into my hands, but it is only within the last four years, that, thanks to Dr. Gordon, I have been able to obtain satisfactory evidence as to the nature of the posterior lumbar, and of the sacral vertebræ. This evidence is yielded by a shattered block of Lossiemouth sandstone, which contains the posterior two lumbar vertebræ, with the two sacral vertebræ, of one individual, and very nearly in their natural relation to one another. The first caudal is also present, but it is slightly displaced; and, near the first caudal, there lies the centrum of a vertebra which belongs to the middle region of the tail. The impression of a scute on one portion of the block leaves no doubt that the whole of the vertebræ belong to *Stagonolepis*. Most of the osseous substance of the vertebræ has disappeared, and the specimen is in such a condition that it would be difficult to give intelligible drawings of it. On the other hand, since it is broken in such a manner as to give sections in various directions,

the data obtained by these sectional views may be so combined as to restore all the essential features of the bones with sufficient accuracy (Plate X. [Plate 17] fig. 10).

The centrum which is best preserved is that of the hinder lumbar vertebra. It is 1·9 in. long, and its terminal articular surfaces are 1·8 in. broad by not more than 1·4 in. dorso-ventrally. The articular surface is rather deeply excavated, and has a transversely elongated oval form. The middle part of the centrum is constricted, so that the whole centrum has somewhat the shape of a dice-box. The centra of the two sacral vertebræ are similar in form and dimensions to that of the last lumbar, though less constricted; and they are not ankylosed together. The cast of the centrum of the first caudal vertebra has been somewhat distorted, but it appears to have differed from that of the second sacral in being somewhat shorter. Nothing is left of the centrum of the penultimate lumbar vertebra.

The spinous processes of the lumbar and sacral vertebræ are short and stout, while their dorsal ends are thickened and expanded, as if for the attachment of the scutes of this region. The transverse processes of the penultimate lumbar vertebra are strong, flattened dorso-ventrally, and very slightly recurved, but not inclined dorsally or ventrally. Their antero-lateral angles are rounded off; hence, at their free extremities, they are slightly narrower than at their origins. The distance from the free end of the one to that of the other is about 7 inches.

In the last lumbar vertebra, the transverse processes, though still flattened dorso-ventrally, stand straight out, and are broader at their truncated free extremities than at their origins. In fact, the antero-posterior measurement of the free end is 1·8 in., or nearly the same as that of the centrum of the vertebra. The ribs of the anterior sacral vertebra are strong flattened bones connected with almost the whole length of the centrum and arch; they widen, as they pass outwards, until the free ends measure 2·5 in. antero-posteriorly. The outer ends of these ribs are truncated obliquely, the surfaces for the articulation of the ilia being directed outwards and backwards. The ribs of the second sacral vertebra are still broader, their concave posterior edges sloping rapidly backwards. Their articular surfaces are directed outwards and forwards, meeting those upon the ends of the ribs of the first sacral vertebræ at an obtuse angle. In the first caudal vertebra the spine is more slender, both absolutely and proportionately to the centrum, and rather longer than in the sacral vertebræ. The free end is not expanded.

The characters of the caudal vertebræ in the anterior half and

middle of the tail are very well shown in Plate III. [Plate 10] fig. 2, Plate IV. [Plate 11], figs. 2 and 4, and Plate VII. [Plate 14], fig. 7.

The centra of these vertebræ are all more or less constricted, and have concave anterior and posterior faces of a vertically elongated oval form. Facets for the articulation of the subvertebral bones are visible, on the ventral side of both the anterior and posterior articular surfaces, but they are more marked on the posterior face. In the anterior moiety of the caudal region, the spines are strong but somewhat short, the total height of the vertebræ not exceeding three times that of the vertical diameter of the anterior face of the centrum. The anterior edge of the spine slopes more or less backwards.

Such remains of the subvertebral or chevron bones, as are preserved in the cast of the caudal fragment, show that they were long and slender (Plate IV. [Plate 11] fig. 4).

The centra are not ankylosed with the arches of the vertebræ, but are connected with them by rugose synchondrosial faces (Plate III. [Plate 10] fig. 2). There is no trace of any suture between the transverse processes and the neural arches. In the only posterior caudal vertebra I have seen, the spine has altogether disappeared, and there are no certain indications of transverse processes (Plate VII. [Plate 14] figs. 4, 4a). This vertebra may not belong to *Stagonolepis*.

3. *The reconstruction of the Vertebral Column of Stagonolepis from the foregoing data.*

In a specimen of *Crocodilus biporcatus*, 82 inches long, the skull measures 11·5 inches; the nine cervical vertebræ, 9 inches; the series of 15 thoraco-lumbar vertebræ, 18 inches; the two sacral vertebræ, 2·5 inches; the 35 caudal vertebræ, 41 inches, in length. Including the posterior convexities, the centra of the axis, and of the following five cervicals, are each 1 inch long; while those of the eighth and ninth vertebræ are a little shorter, or about 0·9 inch.

The transverse diameter of the centrum of the third cervical is 0·75 inch, its vertical diameter 0·7 inch. The transverse diameter of the ninth cervical is 1·3 inch, its vertical diameter 0·85 inch. The centra of the thoraco-lumbar vertebræ are all about 1·1 inch in length, and 0·7 inch or 0·75 in vertical diameter. The articular faces of the first thoracic and of the last lumbar centrum are broader (1·0 inch) than the fifth thoracic, which is about 0·7 inch. As far as the ninth thoraco-lumbar, the transverse processes of these vertebræ are inclined, though very slightly, upwards and backwards; those of the tenth, eleventh, and twelfth vertebræ stand straight out; those of the thirteenth and

fourteenth are slightly recurved, while those of the fifteenth pass directly outwards.

The distance between the extreme ends of the transverse processes of the first thoracic vertebra is 2·7 inches. This distance goes on increasing to the ninth, when it reaches 4·25 inches, and then diminishing to the last lumbar, where it is only 3·1 inches.

The extreme distance between the ends of the anterior sacral ribs is 4·5 inches; between those of the posterior sacral ribs, 3·8 inches. The centrum of the first caudal vertebra is 1·1 inch long, and about 0·7 inch in vertical measurement; in the fourth the length is somewhat greater (1·2 inch), and this length is kept up to the posterior fourth of the tail. The vertical measurement diminishes to 0·4 in the middle of the tail, and becomes still less towards its extremity.

The sacral vertebræ of *Stagonolepis* above described, therefore, are larger than the corresponding vertebræ of a *Crocodilus biporcatus*, 6 feet 10 inches long, in the ratio of 19 to 12; and if the proportions of this Crocodile were retained throughout the vertebral column of *Stagonolepis*, the largest thoracic vertebræ (Plate V. [Plate 12] fig. 2) yet met with, the centrum of which is only 1·3 inch long, is too small, by at least a third, to have belonged to an individual of similar dimensions. The same remark applies to the cervical vertebræ and to all the caudal vertebræ, which would fit very well into the same series as the thoracic vertebræ, but are too small for the sacrum.

The centra of the cervical vertebræ of the Crocodiles are, on the average, shorter than those of the thoracic series. In the *Crocodilus biporcatus* referred to, for example, the total length of the nine cervical vertebræ is only 9 inches, which gives an average of only one inch for each.

The centrum of the middle cervical vertebra, figured in Plate I. [Plate 8] figs. 6, 6a, is 0·75 inch long, or shorter than in the *Crocodilus biporcatus*, whilst its vertical measurement, 1·1 inch, is greater than that of a corresponding vertebra in the recent Crocodile. Whence it would appear that the neck of *Stagonolepis Robertsoni* was somewhat shorter than that of *Crocodilus biporcatus*, if, as there is every reason to believe to be the case, it contained no greater number of vertebræ.

The distance between the apices of the transverse processes of the lumbar vertebræ in the *Crocodilus biporcatus* is 3·1 inches, or less than half the corresponding admeasurement in *Stagonolepis*, so that the latter had these processes relatively much longer. But, when *Stagonolepis* is compared with *Crocodilus vulgaris* this difference in the length of the transverse processes of the lumbar vertebræ does not exist; in fact, these and the sacral vertebræ of *Stagonolepis* have very nearly

the dimensions of the corresponding bones in a Nile Crocodile, 114 inches long, in the Museum of the University of Oxford.

Moreover, there is another interesting point of resemblance between the vertebral column of *Stagonolepis* and that of the Nile Crocodile. From the tenth (or first thoracic) to the fifteenth (fifth thoracic) vertebræ inclusively, in the latter, the transverse processes are inclined obliquely upwards and backwards, to a far greater extent than in *C. biporcatus*, the inclination being most marked in the four most anterior thoracic vertebræ; while from the fifteenth vertebra backwards, the transverse processes trend almost directly outwards, or are horizontal.

In *Stagonolepis*, this character of the anterior thoracic vertebræ is somewhat exaggerated; but the remains of the penultimate lumbar vertebra show that as in the Nile Crocodile, the transverse processes become horizontal in the posterior moiety of the præsacral region.

In the *Crocodilia* with complete dermal shields, each transverse row of dorsal scutes in the thoracic region answers to a vertebra (Plate XII.) [Plate 19]; consequently, the average antero-posterior dimensions of such a scute will be equal to the average length of the centrum of a thoracic vertebra, plus a certain addition for the overlapping and overlapped edges. Hence the scute, which answered to the thoracic vertebræ belonging to the specimen of *Stagonolepis*, the sacrum of which has been described, should have measured somewhat more than 2 inches antero-posteriorly.

As I have stated above, the largest dorsal scutes I have met with measure 2·5 inches in antero-posterior length, and, therefore, are large enough to have belonged to a *Stagonolepis* of the size indicated by the fragmentary sacrum.

The Ribs.—Only a few ribs have been obtained, and these were always in a very bad state of preservation, or mere casts. Fig. 6, [Plate 14] Plate VII., represents the reproduction of the cast of the proximal end of an anterior vertebral rib from Findrassie. Fig. 5 on the same Plate is part of a more posterior vertebral rib from Lossiemouth, half the natural size. The capitular and tubercular facets are disposed in the same way as in the Crocodiles, and the face of the rib is concave from side to side. Measured in a straight line from one end to the other, the rib represented in Fig. 5 had a length of 9 inches, and a breadth of 0·6 inch. A fragment of a rib, which is complete at neither end, embedded in the same block of sandstone as the sacral vertebræ, is also 9 inches long and nearly 0·6 inch wide at its narrowest part. The one edge of this rib is straight throughout; but, at about 2 inches from one end, the outer edge

becomes convex, and the breadth of the rib gradually increases to 1·0 inch, but narrows again towards the end of the rib.

Another fragment, imperfect at each end, of about the same length, shows that one face of the rib presented a deep groove separating the outer margin from the rest of the surface of the rib, which is strongly convex. The groove and the convexity occupy the vertebral or proximal half of the rib, the sternal half of the same face being flattened.

I have met with no traces of sternal ribs or sternum ; but it was hardly to be expected that mere calcified cartilages should be preserved under conditions which have been so unfavourable to the conservation of even the most complete bone.

The length of the chord of the curve of the largest vertebral rib of the *Crocodilus biporcatus* is 4·1 inches. Thus the vertebral ribs appear to have been longer in proportion in *Stagonolepis*; though, in the absence of the vertebræ to which they were attached, it is impossible to arrive at any safe conclusion on this head.

4. *The Skull of Stagonolepis Robertsoni* (Plate V. [Plate 12] fig. 1. ; Plate IX. [Plate 16] figs. 1, 2, 3).

In my first essay on *Stagonolepis*, I gave a brief description of the impression of a mandible with long and strong teeth from Findrassie, and I stated that I saw no reason to doubt that it might belong to *Stagonolepis*, though positive proof was wanting.

This mandible is figured in Plate IV. [Plate 11] fig. 1, and its nature will be a subject for future discussion. But that it is not the jaw of *Stagonolepis* has been rendered certain by the discovery of fragments of skulls, provided with teeth of a totally different character, associated with bones and scales of *Stagonolepis*, in such a manner as to leave no question that they formed a part of the same animal.

Much mutilated fragments of the anterior region of two skulls one larger than the other, have been met with.

The smaller (Plate IX. [Plate 16] fig. 1, fig. 1a) consists of a sandstone core (Fig. 1) which is a cast of the interior of the frontal region and of the adjacent part of a prolonged rostrum ; its surface exhibits some adherent bone and impressions which show the form of the palatine region. Only so much of the counterpart (fig. 1ª) as covered the anterior dorsal and the left lateral region of the core is preserved ; but it is important because much of the bone which entered into this region still adheres to the sides of the cavity into

which the core is received. It is not easy to give intelligible figures of this fragment; but, by putting together the data derivable from the study of the appearances which it presents, it is possible to determine several important points in the structure of the skull.

The length of the dorsal region of the skull which is preserved is 4·5 inches. In front it is 0·65 wide, but it gradually widens until, at 3·5 inches from the anterior end, it attains the width of 1·8 inch, and this it retains to its extremity.

Viewed sideways (the long axis of the skull being horizontal) the dorsal contour is at first parallel with the axis; it then slopes somewhat abruptly upwards to the point at which the fragment attains its greatest breadth.

The height of the fragment is, in front, 1·1 inch; behind, more than 2 inches. The ventral face is much broader than the dorsal facet behind, so that the sides slope outwards and downwards; in front, the difference of the breadth of the dorsal and ventral faces is less, and the sides of this part, which forms the commencement of the rostrum, are more nearly parallel.

For a distance of 2·5 inches from the posterior end, the outer face of the thick bony mass which forms the roof of the skull is sculptured by irregular radiating elevations and depressions; but in front of this, the surface is smooth.

A very distinct median suture traverses the whole length of the roof, but no other sutures are discernible.

The bony plates which form the roof of the anterior, narrower, rostral part of the skull (Plate IX. [Plate 16] fig. 1ª, *a*) are flat and 0·15 inch thick; and, for a distance of 1·9 inches from the anterior end, their outer edges are well defined and rounded, and form the dorsal boundary of a vacuity which lies at the sides of the rostrum (Plate IX. [Plate 16] fig. 1ª, *b*). The posterior boundary of this rostral vacuity is formed by the anterior concave edge of a broad plate of bone continuous with the roof above, which passes downwards and a little outwards, and constitutes the lateral wall of the skull behind the vacuity, becoming very thick inferiorly. Thus it is clear that, on each side of the rostrum there was an elongated aperture which measured not less than 0·6 inch vertically; while, antero-posteriorly, it was certainly 1·9 long and may have been much longer. This aperture may be termed the *rostral vacuity*.

The dorsal half of the broad plate of bone, which bounds the rostral vacuity behind, passes into the side walls of the cranium; but its ventral half presents a free edge, concave backwards (Plate IX. [Plate 16] fig. 1ª, *d*), which formed the anterior boundary of a large fossa,

the inner wall of which is constituted by the parietes of the cranium, while the posterior boundary consists of a broken pillar of bone, which extends downwards and outwards from the posterior end of the broad part of the skull. The outer boundary of this *lateral fossa* is for the most part destroyed, but it is evident that it was strong and outwardly arched. Remains of teeth attached to the arch are traceable in its fore part and a mandibular tooth is adherent to its middle. The two rami of the mandible, the impressions of some of the teeth of which are traceable, converged to their symphysis in front of the anterior end of the fossa.

The oral face of the rostrum (Plate IX. [Plate 16] fig. 1, *a*) is preserved for a little more than an inch from its anterior end. In the middle, it presents a raised longitudinal ridge marked in the centre by a narrow groove. On each side of this ridge the surface is slightly excavated from side to side. The alveoli, with the teeth, have vanished, a broken surface of bone occupying their place. In the middle line, the bone which constitutes the floor of the rostrum, for this distance, is continued backwards in the form of two slender, almost vertical plates, between which the anterior end of a thick elongated median osseous style divided into two portions by a deep groove is received (Plate VIII. [Plate 15] fig. 1, *b*). On each side of the central style thus constituted is a large oval opening (Plate IX. [Plate 16] fig. 1, *c*), the anterior part of which lies under the posterior portion of the lateral aperture of the rostrum; these are, without doubt, the posterior nares. They are bounded behind by the impressions of the concave anterior edges of the palatine bones. The impressions of the palatine faces of these bones are at first inclined forwards as well as downwards, so that the edges which bound the posterior nostrils must have been much nearer the dorsal surface of the skull than the alveolar margin of the maxillæ. But they are united with the inner faces of the maxillæ laterally; and, posteriorly, they come to the level of the maxillæ and probably pass into the pterygoids.

An indication of an irregularly oval post-palatine foramen lies between the impressions which indicate the positions of the maxillæ, the posterior part of the palatine, the pterygoid, and the transverse bone.

The especial interest which attaches to this fragment of a skull lies in the fact that it affords trustworthy evidence of the manner in which the primitive posterior nares were constituted in *Stagonolepis*.

The primitive posterior nares are situated far forwards as in Lizards, and neither the palatine nor the pterygoid bones send off those prolongations which, in existing *Crocodilia*, surround the nssal passages, and give rise to the secondary posterior nares, placed far

back, beneath the basisphenoid. Nevertheless, the arrangement of the bones which surround the posterior nares is still distinctively and characteristically crocodilian.

In recent *Crocodilia*, the pterygoid is ankylosed with its fellow in the middle line, and thus gives rise to a large single bone which may be distinguished into a median "body," and five processes, one anterior and four lateral. The dorsal face of the body is inclined somewhat backwards; it is excavated from side to side, and presents numerous ridges and furrows by which it articulates with the ventral and anterior face of the basisphenoid.

In front, it is continued by a sharp longitudinal ridge, which lies beneath the rostrum of the basisphenoid, into the anterior process. This is at first broad, convex from side to side, and furrowed by a deep median groove; but anteriorly the groove grows deeper, and the tapering anterior end of the bone is composed of two thin vertical plates united below, and forming a sheath for the under face of the interorbital or presphenoidal cartilage.

The edges of this anterior, or *palatine* process, of the pterygoid unite at first with the palatine bones; then, for a short distance, just where the thin sheath begins, with the descending process of the prefrontal, while the outer faces of the sheath itself are received between the posterior ends of the vomers.

The two principal lateral, or *transverse*, processes of the conjoined pterygoids are exceedingly broad and almost square, with thick external edges and thinner excavated posterior margins. The anterior edge of the transverse process unites internally with the transverse bone, while the outer and posterior edges are free. On the ventral face, along the line of junction of the transverse processes with the body, strong horizontal plates are sent in; and meeting in the ventral middle line, form the inferior wall of the pterygoid portion of the nasal canal. The suture in which they unite persists, and from the junction of the two horizontal plates a vertical plate is sent up, which meets in the middle line with a ridge, which is the backward continuation of the anterior sheath-like process. The posterior part of the nasal passage is thus divided by a vertical septum.

The remaining pair of processes pass up on the sides of the basisphenoid and there articulate with the quadrate bones. These *quadrate* processes are small and flat, smooth externally, but rough internally, where their sutural surface is continuous with that on the dorsal aspect of the body.

Thus, by the most anterior part of its palatine process, the pterygoid furnishes a longitudinal septum to the middle portion of the nasal

canal; behind this, it gives rise, not only to the septum but to the roof of this canal on each side; and, from the base of the median process onwards, it furnishes septum, roof, side walls and floor. It is the portion which forms the roof, together with the adjacent part of the palatine, which in some Crocodiles, and especially in Gavials, becomes dilated, constituting the well-known bulla of the latter.

The dorsal portion of each palatine bone is thin and elongated, and is united by a short ascending process with the descending process of the prefrontal. Behind this, the inner edge of the palatine articulates with the median process of the pterygoid, which thus separates the two palatines from one another. In front, it unites by harmonia with the outer edge of the vomer, and ends by a thin margin, which is concave forwards, and lies far in front of the anterior margin of the orbit. This thin margin bounds the primitive posterior nares behind. At the sides, the dorsal portion curves round, and enters into the lateral walls and the floor of the nasal passage. The horizontal processes, which constitute the floor, join and send up a median process, as in the case of the pterygoids; and this median process uniting posteriorly with the anterior process of the pterygoid; dorsally with the vomer; and anteriorly with the maxillæ, gives rise to the median septum of the anterior portion of the nasal passage.

The vomers are thin, vertically elongated, plates of bone; together they form a sheath comparable to that furnished by the anterior process of the pterygoid, which is received between their posterior ends. In front, they extend for some distance beyond the palatines on to the dorsal surface of the palatine plates of the maxillæ; but they are separated by a considerable interval from the premaxillæ, though these sometimes send back long processes, over the palatine plates of the maxillæ, towards them.

In order to compare the bones thus described with the corresponding bones in *Stagonolepis*, the osseous plates furnished by the pterygoids and palatines to form the lateral and ventral walls of the posterior nasal canals must be cut away. The primitive posterior nares will then be seen to lie between the septum formed by vomers and the anterior process of the pterygoid in the middle, the palatines behind, and the maxillæ in front and at the sides. And it will be seen that the region of the dorsal wall of the skull which is placed directly over them, lies at some distance in front of the orbits, and corresponds, roughly, with the anterior limits of the lachrymal bones.

When the skull of a Gavial is taken for comparison, the position of the primitive posterior nares, in relation to the base of the rostrum and to the hinder maxillary teeth, is seen closely to correspond with

that of the same parts in *Stagonolepis*. The chief difference is that the primitive posterior nares are smaller, the post-palatine foramina larger, and the palatine bones narrower in proportion, in the Gavial, than in *Stagonolepis*. But the median styliform grooved bone in *Stagonolepis* answers to the anterior process of the pterygoid in the Crocodiles, and the lamellar processes on each side of it to the vomers of the recent species; and it is exactly this arrangement which is not met with in Lizards, and is characteristically crocodilian.

Stagonolepis, therefore, has distinctively crocodilian vomers, palatines, and pterygoids, but it differs from existing Crocodiles in the absence of those descending plates which shut off the nasal passage from the mouth in the latter, and give rise to the secondary posterior nares.

The interpretation of the rostral vacuities and of the lateral fossæ is open to doubt.

In the *Teleosauria* (Plate XI. [Plate 16] fig. 1, 1b) there are larger or smaller vacuities at the sides of the base of the rostrum, in the same position as those of *Stagonolepis*. They lie between the nasal and the maxillary bones, and in front of the lachrymals, whence they may be termed *prælachrymal vacuities.*

It is clear that if the rostral vacuities of *Stagonolepis* answer to them, the external nares must have been situated further forward, probably at the end of the rostrum, and the lateral fossæ will be the orbits.

But in *Belodon*, with which *Stagonolepis* has many and close affinities, the anterior nares are situated in a position corresponding with the rostral vacuities of *Stagonolepis*, though much closer together, on account of the extreme narrowness of the intervening portion of the nasal bones; while the prælachrymal vacuities, which are of enormous size, occupy the position of the lateral fossæ of *Stagonolepis*.

With the materials at hand, I do not think it is possible to decide positively whether *Stagonolepis* followed the type of the *Teleosauria*, or that of *Belodon*, but the probabilities seem to me to be in favour of the latter supposition. Whichever interpretation be adopted, the interesting fact results that, by its skull, *Stagonolepis* forms a link between the *Teleosauria* and *Belodon*. For, if the rostral vacuities are anterior nares, as in the latter genus, the breadth of the nasal bones between them is an indication of less divergence from the Teleosaurian than occurs in *Belodon*; and, if they are prælachrymal vacuities, their size, so much larger than in any known Teleosaurian, is an approximation to the characters of *Belodon*.

The other fragment of a cranium, of considerably larger size, is figured in Plate V. [Plate 12] figs. 1, 1ª, 1ᵇ. A maxilla (*b*) bears the remains of nine teeth, and indistinct impressions of two others. The

hinder are smaller than the anterior teeth. All have swollen crowns, marked off by a constriction from the cylindrical fang. The crowns of the fifth and sixth teeth present flat surfaces produced by wearing against the teeth of the lower jaw. The inner part of the bone is much crushed, except in front, where its margin shows a natural edge (*a*) concave inwards. Posteriorly, the extremity of the maxilla passes into a curved osseous mass, which is indistinguishably crushed into the end of a long and flat, but thick bone (*c*), which lies on the left side of the figure. The fossil is broken along the oblique line which runs from the first tooth in front and on the right side, backwards and to the left; and when the piece which lies in front of the line of fracture is removed, the fossil presents the appearance represented in fig. 1^a. The natural edge of the long flat bone (*c*) curves outward in front, and joining with an ascending plate from the maxilla bounds an oval vacuity (*Or*) of which the anterior contour only is traceable. When the piece of the fossil which has been removed is turned round so as to show its dorsal face (fig. 1^b), it exhibits the ascending process of the maxilla (*d*), and the impression of the anterior part of the long flat bone (*c*) with the space (*Or*) which they partially inclose. Moreover, by clearing away the matrix in front of this, I exposed a fan-shaped plate of bone (fig. 1^b, *Vo*) broken in front, but with a natural free edge, which looks outwards and backwards. This bone is continued backwards into a laterally compressed vertical plate (*f*), the ventral edge of which is seen in fig. 1.

It is not easy to interpret this fossil in perfect consistency with the structure of the skull, as already made out in the less disturbed fragment. But the most probable reading appears to me to be, that fig. 1, in front of the line of fracture, presents a view of the anterior boundary of the posterior nostril; while, behind the line of fracture, it shows the inner surface of the bones (*c*), which occupy the median line of the roof of the skull, and which must be either nasals or frontals.

Figures 1^a and 1^b give a view of the dorsal aspect of the skull, and show the anterior boundary of the oval space (*Or*) bounded in front by the ascending process of the maxilla (*d*). I was at first inclined to regard the space as the orbit; but I think it is more probable that it is the prælachrymal vacuity.

The fan-shaped bone must be the vomer, as it bounds the primitive posterior nostril internally and anteriorly, and is continued back into the vertical lamina, which separates the two nares.

However doubtful may be the interpretation of other parts of this fragment, it confirms the conception already formed of the structure of the posterior nares.

The Mandible.—Evidence respecting the form of the mandible is afforded by the specimens figured in Plate I. [Plate 8] fig. 4, 4^a, and Plate VI. [Plate 13] fig. 3 and 3^a. The former figure represents a portion of the two rami of the mandible close to the symphysis. At the left-hand extremity, the ventral edge of the ramus is entire, and it measures 0·7 inch vertically; at the opposite extremity the contour of a transverse section is shown with a tooth in its alveolus. (Fig. 4^a). This tooth is 0·7 long. In the adherent fragment of the upper jaw the remains of four teeth are seen, and it may be concluded that the fragment of the mandible, which is 2 inches long, bore six teeth.

In Plate VI. [Plate 13] figs. 3, 3^a are the remains of a series of teeth, belonging apparently to the two rami of the mandible, for some distance before and after their junction in the symphysis. In this jaw, nine teeth occupy about 2·5 inches.

From these specimens, imperfect as they are, it may be concluded that the rami of the mandible were united in a long symphysis, as in existing Gavials and in *Belodon;* and this is what might be expected from the elongation of the snout.

5. *The Teeth of Stagonolepis Robertsoni* (Plate I. [figs. 4 and 4a; Plate V. [Plate 12] figs. 1 and 1^c, 1^d, 1^e; Plate VI. [Plate 13] fig. 3^c; Plate IX. [Plate 16] figs. 3, 4, 4^a). Many teeth have been met with in close association with portions of *Stagonolepis*, or in the jaws. Putting together the information yielded by the specimens figured in Plate V. [Plate 12] fig. 1, and Plate VI. [Plate 13] fig. 3, it may be safely concluded that there were not fewer than twenty teeth on each side in each jaw. There is no evidence respecting the form of the most anterior teeth. The middle and posterior teeth are all very similar. The fang is subcylindrical, and is excavated by a large pulp cavity, as in Crocodiles. The crown is of a pear shape, tapering up towards an obtuse point. In section it is circular or broadly oval, except towards the apex, where it becomes lenticular. Even here, however, the anterior and posterior margins are not produced into ridges, and it is only in some teeth that a few inconspicuous and obtuse elevations, which may represent serrations, are to be observed (Plate IX. [Plate 16] fig. 4^a).

The surface of the enamel is raised into irregular longitudinal folds separated by shallow grooves. Not unfrequently the crowns of the teeth present oval, flattened surfaces, obviously produced by wearing against the opposed teeth (Plate V. [Plate 12] figs. 1^c, 1^d).

These teeth are, in fact, very similar to the hindermost teeth in living Crocodiles and Alligators.

The hindermost teeth in the maxilla are more slender than the others, and probably the same modification obtained in the teeth of the mandible. In the absence of the anterior portion of either upper or lower jaws, it would be unsafe to say that the foremost teeth might not have been elongated and sharp pointed, but it is exceedingly unlikely that they could have even approached the form and size of such teeth as those represented in Plate IV. [Plate 11] fig. 1.

6. *The Bones of the Pectoral and Pelvic Arches and Limbs.*

Not a single entire bone belonging to these portions of the skeleton has presented itself. All are more or less broken, and the most instructive specimens are mere casts in sandstone. Under these circumstances the work of reconstruction has presented many difficulties, and it is only recently that I have been able to make sure of the structure of the pectoral arch and of the pelvis, and of the characters of some of the chief bones of the limbs.

The Scapula and the Coracoid.—The impression of the inner face of a scapula, of which a cast is represented in Plate VIII. [Plate 15] fig. 3, is accompanied by impressions of scutes of *Stagonolepis* in a block of Findrassie sandstone; while the coracoid figured in the same Plate (fig. 1) is lodged in a large mass of Lossiemouth sandstone and is also accompanied by several dorsal scutes, all of which measure 5·5 inches in width by 2·5 inches in anteroposterior diameter. It may therefore be concluded that this coracoid belonged to one of the largest examples of *Stagonolepis*.

The scapula presents its smooth inner face, which is slightly concave from above downwards, to the eye. It is expanded at both ends, the dorsal extremity being thin, while the ventral end becomes very thick posteriorly, where it presents an obliquely truncated articular face which formed the dorsal half of the glenoidal cavity. In front it thins off, and is continued into a broad thin process, the anterior extremity of which seems to be imperfect. The ventral edge of the scapula presents a rough surface, broad behind and narrow in front, for articulation with the coracoid.

The vertical or dorso-ventral measurement of this bone is 5·6 inches. The greatest antero-posterior measurement of the dorsal end 1·95 inch, of the ventral end 2·55 inches; the greatest thickness of this end, 0·85 inch.

The *Coracoid* (Plate VIII. [Plate 15] fig. 1) was almost wholly

covered up by the matrix when it came into my hands; but careful chiselling away of the sandstone rendered visible an irregularly oval plate of bone, 4·8 inches long by 3·3 inches at widest, bounded on the one side by a regularly curved natural margin, while on the other it was much broken. As the bone is figured, its thickest part corresponds with the lower half of the broken portion, the upper half being thin. Just above the thick broken portion, a circular hole (0·3 inch) is seen. Regarding this as the homologue of the foramen in the coracoid of a Crocodile, I considered that the thick broken edge must correspond with the position of the glenoidal head of the coracoid, and consequently that the entire curved edge of the bone answered to the inner margin of the coracoid, or to that part of it which articulates with the sternum in a Crocodile. But if such be the case, it follows that the coracoid of *Stagonolepis* is very different from that of any known recent or fossil Crocodile, except *Belodon*; in which, so far as the generally oval form of the coracoid is concerned, a similar modification obtains. Von Mayer states that, in one of his specimens of the pectoral arch of *Belodon*, the scapula and coracoid were ankylosed. The scapula of *Stagonolepis*, already described, on the other hand, seemed to show that no such ankylosis occurred in this genus. Singularly enough, however, a more recently discovered fossil proves that ankylosis of these bones also occurs in *Stagonolepis*,—even in animals of smaller dimensions than that to which the coracoid represented in Plate VIII. [Plate 15] belonged.

This important specimen (Plate X. [Plate 17] fig. 1, 1[a]) lies on one face of a block of Lossiemouth sandstone, along with an ischium which crosses it, while at no great distance on the underside of the block, there is an ilium. The total length of the two bones, from the ventral edge of the coracoid to the utmost limit to which the dorsal edge of the scapula can be traced is 9·9 inches. The centre of the glenoidal cavity is 2·5 inches from the centre of the ventral margin of the coracoid, and as the line of this measurement corresponds pretty nearly with the transverse diameter of the coracoid, Plate VIII. [Plate 15] fig. 1, it is clear that the latter bone is the larger. The same conclusion is derivable from the difference between the distance from the centre of the foramen to the summit of the convexity of the posterior edge, which is 2·5 inches in this coracoid, and 2·75 inches in the previously described bone.

In the present coracoid, the ventral edge is evenly curved from the glenoidal cavity to a line corresponding with the long axis of the ankylosed bones and drawn through the foramen. At this point, the ventral edge is met by the obliquely truncated, probably fractured

anterior margin, which then becomes nearly straight and meets the anterior edge of the scapula at an angle. The circular foramen is situated in a line drawn from this angle to the centre of the glenoidal face. The latter is concave from above downwards, convex from side to side, and looks outwards as well as backwards. Below it is bounded by a very prominent lip. The dorsal end of the scapula expands more rapidly than in the specimen already described, and attains a greater length than is indicated by the cast of the latter. Moreover, the form of the anterior process at the glenoidal end of the scapula differs in the two cases.

The scapula in the last-mentioned specimen has, as nearly as may be, twice the dimensions of the same bone in the *Crocodilus biporcatus*, 7 feet long.

The Interclavicle.—This bone, of which only one specimen has been met with, is represented of the size of nature in Plate X. [Plate 17] fig. 2, and a side view of it is given in fig. 2a of the same Plate.

On comparing it with the corresponding bone (generally termed the sternum) in the skeleton of the *Crocodilus biporcatus*, which has already served as a standard of comparison, it is seen to correspond with the posterior two-thirds of the latter in its general form and dimensions. However, it is slightly smaller, thinner, and more curved, and there is a more marked constriction between the posterior spatulate, and the anterior thicker and laterally grooved portion of the bone.

The Ilium.—The bone, represented about three-fourths of the natural size in Plate VI. [Plate 13] fig. 1, lies in a large block of Lossiemouth sandstone along with the femur represented in same Plate (fig. 2), ribs, fragments of vertebræ, and numerous dorsal scutes, the largest of which is 5·25 inches wide by 2·25 inches antero-posteriorly. It is much broken, and consists of two divisions separated by a median constriction; the one division having a semi-circular, the other a straight free edge. The total length of the bone, measured between lines drawn at right angles to the straight edge, is nearly 9 inches, while its greatest transverse diameter is 5·8 inches. For a long time, I took this bone to be a coracoid, but better specimens, which have come under my notice, prove it to be a right ilium of which only the injured inner face is displayed.

Two almost perfect impressions of the outer face of the ilium, both belonging to the right side, but one considerably larger than the other, have been obtained at Lossiemouth (Plate X. [Plate 17] figs. 3 and 4).

The wide and shallow acetabular cavity occupies all that part of the external face of the bone which in the specimen figured in Plate VI. [Plate 13] is terminated by a semicircular edge. But it is seen that the corresponding edge of the perfect ilium is not truly semicircular, but is formed by two edges, one antero-inferior and the other postero-inferior. The postero-inferior edge is undulating, the antero-inferior straighter; but the two edges meet in an obtuse angle, and there is no trace of any notch or excavation in this border of the bone.

On the dorsal side, the acetabular cavity is bounded by a sharp projecting ridge continuous with its roof. In front, this passes gradually into the outer face of the thick and rounded pillar which bounds the acetabulum anteriorly. Behind, on the other hand, the ridge ceases suddenly at the level of the neck by which the ala of the ilium passes into its acetabular portion; so that a sort of shallow and broad notch lies between the end of the ridge and the thickened extremity of the posterior pillar, or hinder margin of the acetabular cavity. At the free ends of the two pillars, the ventral margin of the acetabular wall is very thick and rugose, that of the anterior pillar being half as large again as that of the posterior. Between these two the rest of the edge is thin.

The ala of the ilium, into which the acetabular portion of the bone passes dorsally, answers to the straight-edged division of the specimen figured in Plate VI. [Plate 13], and is equal to about half the entire bone. The outer face is slightly excavated, and presents radiating striæ near its dorsal edge. The anterior half of the dorsal margin runs nearly parallel with the dorsal margin of the acetabulum. The anterior margin is long and concave forwards, so that the antero-superior angle is somewhat produced. The thick posterior margin, which is bevelled off to a flat surface above, is much more inclined than the anterior, and the postero-superior angle of the ilium is consequently much more prolonged than the antero-superior angle.

The following are the measurements of the ilia, No. I. being the specimen figured in Plate VI. [Plate 13] and Nos. II. and III. the larger and the smaller ilia just described:—

	I.	II.	III.	Crocodilus biporcatus.
	ins.	ins.	ins.	ins.
Length of the dorsal margin of the ala	6·5	5·9	4·2	3·0
Vertical height of the ala, measured from the middle of the outer edge of the acetabulum . .	—	2·1	1·5	0·8
Antero-posterior diameter of the "neck" . . .	3·2	3·5	2·5	1·9
Outside antero-posterior diameter of the acetabular portion	—	5·2	3·75	2·3

No. I. therefore is rather larger than No. II., and No. III. has about two-thirds of the size of No. II., while the latter is about twice as large as the corresponding bone of the *Crocodilus biporcatus*. The cast of No. III. lies on the under side of the block of sandstone, on the upper side of which, and separated from it only by a few inches, are the ankylosed scapula and coracoid, already discussed, and an ischium to be described immediately; so that there can be little doubt that all these bones belonged to the same animal.

It is obvious, from the form of the acetabular region of the ilium, that it must have constituted the greater part of the inner wall of the acetabulum, and that the segments of that wall which were furnished by the pubis and the ischium must have been relatively small.

The Ischium.—This bone (Plate X. [Plate 17] fig. 5, 5[a]) has, roughly speaking, the form of a triangle, the base of which is formed by its anterior edge, while the two other sides are represented by the ventral and the dorsal edges. The latter is thick, rounded, and somewhat excavated, while the ventral edge is very thin. The apex or posterior extremity of the triangle is truncated and thick. The ventral half of its base, or anterior side, is formed by a thin curved edge, which bounded the obturator space behind. The dorsal half is constituted by an elongated articular surface, which looks upwards and forwards, and is concave from above downwards, and from side to side.

This surface is 2·6 inches long, but is nowhere more than 0·7 wide. Its outer side is bounded by a thick lip, which is very prominent at its dorsal extremity, but rapidly dies away and disappears, at about half an inch from the ventral end. The inner edge of the articular surface appears to have been thin, and has an undulating contour. Where this segment of the acetabulum ends and the thin edge which bounds the obturator foramen commences, the latter presents an elongated facet 0·3 inch long, which would seem to have articulated with the pubis. At the dorsal end of the acetabular facet, the bone is thick and presents a broad surface for articulation with the posterior pillar of the acetabular portion of the ilium.

The outer or ventral face of the ischium is concave and is marked by striæ which are particularly conspicuous towards the ventral edge. The inner surface is slightly convex. The extreme length of this bone is 7 inches, its extreme width 4·2 inches.

The length of the acetabular articular surface of the ischium corresponds very closely with that of the postero-inferior, or ischial, portion of the ventral margin of the acetabulum, in the smallest of the three ilia; and, as this ilium was found close to the ischium, I cannot

doubt that they belong to the same animal, although the large size of the ischium in proportion to the ilium is somewhat remarkable.

The Pubis.—The only bone which I can regard as the pubis is that of which the most perfect specimen I have seen is figured, of the natural size, in Plate VIII. [Plate 15] fig. 2. It is accompanied by the impression and part of the osseous substance of a scute. It is 6 inches long, flattened, comparatively narrow, and thick in the middle and wide at each end, the wider end having a well-defined convex margin and becoming very thin; this was indubitably the ventral or symphysial edge of the bone. One of the other two entire edges of the bone is longer and less excavated than the other, and I conceive it to have been anterior. The dorsal, or acetabular, end of the bone is much broken, but its anterior end was obviously thick, while posteriorly it was produced into a broad prolongation, which is thin and shattered towards its free end.

I suppose this process to have entered into the inner wall of the acetabulum, as in *Lacertilia.*

Whatever doubt may rest upon the character of the acetabular end of the pubis, the structure of the ilium and of the ischium conclusively proves that the inner wall of the acetabulum was formed by the union of all three pelvic bones, and that there was no vacuity, or notch, such as exists in the ilia of recent *Crocodilia* and of the *Ornithoscelida.*

The Femur.—On the same block of sandstone with the ilium figured on Plate VI. [Plate 13] fig. 1, and close to it, lies the elongated bone represented in fig. 2 of the same Plate, in the position which it occupies relatively to the ilium. This bone has a length of very nearly 12 inches, while the end nearest the ilium, which is plainly the proper proximal end, is 3·5 inches broad. It is flattened and has a nearly straight margin, with the outer angle rounded off. From the proximal end, the bone gradually narrows to the middle of the sub-cylindrical shaft, which has a diameter of 1·5 inches. At the distal end it is hardly wider, but it is probable that part of the bone is broken away.

The exposed face of the proximal half of the bone is convex, that of the distal half concave, as the accompanying contour fig. 2a shows. On the free surface of the distal end there is a slight depression, indicating the commencement of the division between the condyles.

It will be seen from the table of measurements of the ilia, given above, that the ilium, in association with which this bone was found, was about twice the size of that of the 7-foot specimen of *Crocodilus biporcatus.* Now the femur of this Crocodile is just

6 inches long, so that the bone in question has the proportions that might be expected, if the limbs of *Stagonolepis* resembled those of ordinary Crocodiles.

In the Crocodile, the extreme width of the proximal end of the femur is 1·45 inches, that of the distal end 1·4 inches, or practically the same. Moreover, the plane of the proximal end of the bone is inclined at an angle of 45° to that of the distal end. Hence, when the two condyles rest on a flat surface, the dorsal face of the proximal end looks outwards and backwards, and its ventral face in the contrary direction.

The femur of *Stagonolepis* presents no such torsion ; and, in this respect, as in the narrowness of the distal, relatively to the proximal end, it differs from the same bone in Crocodiles and in Lizards.

It may be suggested that the femur of *Stagonolepis* has been crushed and distorted, but another femur figured of half the size of nature in Plate VII. [Plate 14] fig. 8, presents the same peculiarities.

The Humerus.—Such being the characters of the femur, the bone represented in Plate VII. [Plate 14] fig. 7, can only be a humerus, though at first sight it looks much more like a femur. I have unfortunately no complete example of this bone, though three specimens of it, two large and one small, have come into my hands. That figured in Plate VII. [Plate 14] fig. 7, is a gutta percha impression of a cast, which lies along with that of the bone represented in Plate VIII. [Plate 15] fig. 4, and with casts of dorsal and ventral scutes, of a rib, and of what appears to be a phalanx, in a block of Findrassie sandstone. The largest of these scutes do not measure more than 1·75 inches antero-posteriorly by 4 inches in width; whence the animal to which they belonged is by no means of the largest size. The scute represented in Plate II. [Plate 9] fig. 1, is one of those on this block. I may mention that it was the discovery of this fossil which first led Dr. Gordon to suspect the reptilian nature of *Stagonolepis*.

The distal end of the bone measures about 2·7 inches in transverse diameter, and the impression of the shaft and proximal end are traceable for a length of 7·3 inches. The impression of a second and larger specimen of a similar bone, from Lossiemouth, measures 9·9 in length, and was probably considerably longer, the distal end having a diameter of 3·5 inches. On what appears to have been the radial side of the bone there is a projecting ridge separated by a groove from the shaft, which terminates by a rounded free edge opposite the middle of the larger condyle. A similar ridge is observable in the humeri of Lizards, *Chelonia*, *Dicynodontia*, and of *Belodon*.

The impression of a smaller humerus (Plate X. [Plate 17] fig. 7) measures 7·3 inches in length, and only a very small portion can be wanting in the middle of its proximal end. The distal end and the shaft are nearly complete, but the articular head at the proximal end is broken away. The distal end measures 2·5 inches in transverse diameter, and the middle of the shaft about one inch; while what remains of the flattened proximal end is rather wider than the distal extremity.

If we take the proportions of this bone as a standard, the whole length of the humerus should be about three diameters of the distal end, which will give the following dimensions for the three humeri taking them in the order of size:

	I.	II.	III.	Crocodilus biporcatus.
	ins.	ins.	ins.	ins.
Distal end	3·5	2·7	2·5	1·55
Total length	10·5	8·1	7·5	5·5

In the *Crocodilus biporcatus*, the extreme length of the humerus is 5.5 inches, the extreme breadth of the proximal end 1·45 in., and of the distal end 1·55 in. Hence the length of the bone in proportion to the latter diameter is as about 3½ to 1.

Thus the distal end of the humerus is slightly broader in proportion to its length in *Stagonolepis*, and, so far as any judgment can be formed from the specimens of femora, much broader in proportion to the distal end of the femur than in *Crocodilus biporcatus*; but the longest humerus, like the longest femur, is very nearly twice the length of that of the Crocodile; so that, if the longest femur and the longest humerus had belonged to the same animal, they would have had about the same relative proportions as in *Crocodilus biporcatus*.

In respect of the excess of breadth of the distal end of the humerus over that of the femur, the *Stagonolepis* approaches the Lacertilian type; and the approximation is still more marked in the expansion of the proximal end of the humerus exhibited by the casts figured in Plate X. [Plate 17] figs. 6 and 7, and in the absence of that excavation between the deltoid ridge and the articular head which characterises the Crocodilian humerus.

The Radius or *Fibula*.—Fig 4. [Plate 15] Plate VIII., represents the cast of an impression of a bone which was found along with the humerus, Plate VII. [Plate 14] fig. 7. The *primâ facie* probability therefore is that it belongs to the antebrachium, and, if so, it can only

be the radius. In fact, the shape of the end which is upper in the figure agrees very well with the distal end of the radius in a Crocodile, while the opposite extremity accords with the proximal end. In other respects, the form of the bone is somewhat different; and indeed, if considered in the position in which it is represented, it presents so many points of resemblance to the fibula of a Crocodile that I was, at first, inclined to identify it with the latter bone. The length of this bone is 5·7 inches or 0·76 of the probable length of the humerus which accompanied it. In the *Crocodilus biporcatus* the radius is 3·5 inches long. As the humerus measures 5·5 inches, the radius has only 0·64 of the length of the humerus, and is therefore proportionately much shorter than in *Stagonolepis*.

The fibula of the same Crocodile is 4·25 inches long, or 0·77 to the humerus as 1; which is in close agreement with proportions of the present bone, supposing it to be the fibula. The marked angulation of the anterior contour, in which this bone resembles the fibula and differs from the radius, is, however, situated considerably below the centre of the bone and not midway between the centre and the proximal end, as in the Crocodiles and Lizards. Moreover, while the planes of the articular ends of the bone are sensibly parallel, as in the radius of both Crocodiles and Lizards, the planes of these two surfaces in the fibula of these reptiles are inclined at a large angle. On the whole, the preponderance of the evidence appears to me to be in favour of the interpretation of the bone as a radius.

The bone, represented of the natural size in Plate VII. [Plate 14] fig. 9, lies in a block of Lossiemouth sandstone alongside a dorsal scute of the largest dimensions (5 inches by 2·5 inches). It is 7·5 inches long, and flattened at the ends, both of which are imperfect. The end, which is lower in the figure, is 1·75 in. broad, while the upper extremity is rather narrower. The one edge is evenly curved and rounded, the other is angulated by a projection which lies nearer the upper than the lower end of the bone. I suspect that this is a radius (or fibula) of larger size than the foregoing.

The Tibia (?)—The only specimen of a bone which will answer for a tibia, which I have seen, is that a cast of the impression of which is figured in Plate X. [Plate 17] fig. 8. It is 9·2 inches long, and 1·6 inches thick in the middle of its shaft, which is much bent. The upper end is obliquely truncated, the lower compressed, rounded, and with a well-marked antero-posterior depression, or groove, which divides the articular surface into two portions.

In the *Crocodilus biporcatus*, the tibia is 4·5 long, or 0·75 to the femur as 1; which is, as nearly as may be, the proportion of this

bone to the longest femur of *Stagonolepis*, but of course it may have belonged to one of the shorter femora.

The impression of this bone is so imperfect that it would be unsafe to lay much weight upon the differences in form of the distal end of the cast from that presented by the distal end of a crocodile's tibia. But, if the articular surface for the astragalus has not been distorted, it would appear that this surface was more Lacertilian than Crocodilian in *Stagonolepis*. In fact, in the crocodile, when the trihedral proximal end of the tibia rests on a flat surface, with its obtuse crest turned upwards, the surfaces of the flattened distal end are seen to look respectively outwards and upwards, and downwards and inwards, *i.e.*, towards the axis of the limb. The plane of the distal end of the bone is, in fact, under these circumstances, inclined at an angle of 45° to that of the flat surface on which it rests, as I have shown to be the case in the tibiæ of *Ornithoscelida* and *Aves*. But the articular face itself has nearly the contour of the quadrant of a circle, being convex externally and concave internally. The long axis of that part of the articular surface which lies nearest the fibula is parallel with the surface on which the tibia rests, which the other moiety is elongated from before backwards.

In a Lizard (*e.g.*, *Varanus*), on the other hand, the distal end of the tibia is, like its proximal end, trihedral, and not flattened; in correspondence therewith, its articular surface is triangular in contour, and a broad pulley-shaped groove, which runs from before backwards, divides the inner from the outer projecting ridge. On the whole, therefore, the form of the distal end of the tibia of *Stagonolepis* (if the bone in question is correctly identified), appears to have been more Lacertilian than Crocodilian.

Bones of the feet.—I have met with no carpal or tarsal bones, and only a few imperfect impressions of bones which can be referred to the digits. Of these, one (Plate VIII. [Plate 15], fig. 5) is exhibited by a piece of Findrassie sandstone, which presents no other impressions.

The bone is 2·25 inches long. Its proximal end is 1·15 inches wide, with a truncated articular surface, the exact form of which cannot be made out. The distal end presents a well-marked curved articular pulley, with an antero-posterior diameter of about half an inch.

From the general form of this bone, I think there can be no doubt that it belongs either to the metacarpus or the metatarsus, and to the first præaxial element (pollex or hallux) of the series. Its length is exactly the same as that of the metatarsal of the hallux of the *Crocodilus biporcatus*, and it would be very similar to that bone in form if it were not fully half as broad again.

The metacarpal of the pollex in the Crocodile has a length of only 0·9 inch, and its proximal end is much broader and more expanded, while the carpal articular surface is very convex.

In all probability, therefore, this bone is the metatarsal of the hallux; and if so, its proportions suggest that the hind foot was of a heavier and more massive form in *Stagonolepis* than in recent Crocodiles.

On the same block of Lossiemouth sandstone as that containing the radius, or fibula, figured in Plate VII. [Plate 14] fig. 9, there is the impression of what I take to be a metacarpal bone, the cast of which is represesented of the natural size in Plate X. [Plate 17] fig. 9. On the side of the distal articular head there is, as in Crocodiles, a well-marked pit for the lateral ligament.

The impression of a solitary phalanx 1·15 inch long and 0·4 inch in greatest transverse diameter is to be seen on the same slab as that which bears the impression of the humerus figured in Plate VII. [Plate 14] fig. 7.

In my first paper on *Stagonolepis*, I mention having met with a "single natural cast of a long and nearly straight bone, which I can only regard as an ungual phalanx," indicating "a length of claw wholly foreign to the Crocodilian foot." The bone, as reproduced by taking an impression of the cast in question, is figured in Plate VIII. [Plate 15] fig. 6, of the natural size. The slab in which it occurs exhibits impressions of scutes and an imperfect cast of vertebra, so that there is every reason to believe that the bone formed part of the skeleton of *Stagonolepis*.

The bone is 3·65 inches long, asymmetrical, narrow, and thin at one end, but suddenly widens out and becomes thicker at the other, the extremity of which is obliquely truncated and presents an uneven, but smooth and apparently articular surface (Plate VI. [Plate 13] fig. 6^a). The surface of the expanded part presents many minute pits and grooves, somewhat resembling the pits and grooves which are to be seen on an ungual phalanx of a Crocodile, but there is no strong longitudinal groove such as marks the lateral faces of those ungual phalanges which are ensheathed in claws in the Crocodilia.

The longest ungual phalanx, that of the hallux, in the *Crocodilus biporcatus*, is only an inch long, is more curved and pointed at the apex, and its articular surface is altogether different.

There is no reason to believe that a bone of this character could have formed any part of the exoskeleton, and I am at a loss to know to what part of the endoskeleton it can be referred, except the manus

or the pes. My original supposition, that the bone is an ungual phalanx, is opposed by its great length and by the absence of the lateral grooves; though it might be suggested that it belonged to a digit which, like the two postaxial digits in the Crocodile, was devoid of a nail. In this case, however, the great length of the bone would be even more anomalous.

Perhaps it represents the fifth metatarsal, which, though short and rudimentary in the recent Crocodiles, may well have been larger in so ancient a form as *Stagonolepis*.

III. The Taxonomy, or Systematic Position, of Stagonolepis Robertsoni.

From what has been stated in the preceding pages, it is clear that *Stagonolepis* must have resembled a modern Caiman, with strong limbs, of which the anterior were at least as large in proportion to the posterior as in *Crocodilus biporcatus*, but with a relatively long and narrow skull, like that of a Gavial.

As in the existing Caimans and Jacares, the trunk and tail were provided with ventral, as well as with dorsal, osseous scutes; but the dorsal shield contained not more than two longitudinal series of scutes, and the ventral shield not more than eight such series. The dorsal and the ventral shields were distinct in the trunk, but united together in the tail. The dorsal scutes were angulated and carinated; the ventral scutes were flat and composed of a single ossification.

The vertebræ were amphicœlous: the anterior and posterior faces of the centra being slightly concave. The transverse processes of the anterior thoracic vertebræ resembled the corresponding processes in some recent Crocodiles (e.g., *C. niloticus*) and in *Belodon*, in being much inclined upwards.

The transverse processes of the lumbar vertebræ were long, broad, and directed horizontally; and the free ends of those of the last lumbar vertebra were expanded.

The sacrum consisted of two amphicœlous vertebræ, which were not ankylosed. The free ends of the sacral ribs were remarkably expanded, more so than in any known Crocodile.

The centrum of the first caudal vertebra was amphicœlous, and the subvertebral bones resembled those of Crocodiles.

The anterior region of the skull was produced into a slender rostrum, and the rami of the mandibles united in a long symphysis

The posterior nares were situated far forwards, as in Lizards; and neither the palatine, nor the pterygoid bones, united to prolong the nasal passage backwards and give rise to secondary posterior nares, as they do in existing Crocodiles. In the mode of formation of the primitive posterior nares, however, *Stagonolepis* conformed to the Crocodilian type.

All the teeth which have been found, in juxtaposition with *Stagonolepis* remains, have short and obtusely pointed crowns, like the hinder teeth of existing Crocodiles. They sometimes show signs of being worn down by mutual attrition.

In the pectoral arch, the scapula resembles that of recent Crocodiles; but the coracoid is short and rounded, like that of *Belodon*, of the *Ornithoscelida* and of some Lizards (e.g., *Sphenodon*).

As in Crocodiles, there is an interclavicle; but, apparently, no clavicles existed.

The humerus is more lacertian than that of recent Crocodiles and resembles that of *Belodon*, in the expansion of its proximal end, and in the presence of a ridge, marked off by a groove, on the radial side of its distal end.

The ilium differs from that of Crocodiles in the large size of the ala, especially in front, and in the forward prolongation of its anterior dorsal angle; further, in the shape of the ventral margin of its acetabular portion, and in the absence of any notch or excavation of that margin.

The acetabular end of the ischium is like that of a Lizard and unlike that of a Crocodile; and the rest of the bone is much shorter dorso-ventrally and longer antro-posteriorly than in Crocodiles, in both which respects it resembles *Belodon*.

The distal end of the femur is narrower in proportion to its proximal end, and to the distal end of the humerus, than in existing Crocodiles; in which respect again, *Stagonolepis* resembles *Belodon*.

Among known forms of Reptiles, the nearest ally of *Stagonolepis* is undoubtedly the *Belodon* of the Upper Keuper of Wurtemberg, of which the remains of several species have been made known by H. Von Meyer ("Palæontographica," Bände VII., X., XIV., 1861–1865). Von Meyer describes and figures scutes, vertebræ of various regions (though not of the sacrum); and very perfect crania and teeth; the scapula, coracoid, and humerus; the ilium and the femur; and, when I was in Stuttgart, in 1873, Herr Kapff had the goodness to show me a pelvis, with the ischium in place.

An extensive comparison can therefore be instituted between

Belodon and *Stagonolepis;* and it proves (as I have incidentally pointed out) that the two genera resembled one another in many respects, but nevertheless were separated by highly important differential characters.

That the skulls were exceedingly unlike is sufficiently obvious from the comparison of even such imperfect fragments of the cranium of *Stagonolepis* as have come to light, with the remarkably well-preserved skulls of *Belodon* which are now known. The teeth are widely different; and, as the complete dentition of *Belodon* is known, the difference between the two genera cannot be diminished by the discovery of the teeth of the anterior ends of the jaws in *Stagonolepis*, which may well have been more acuminated than the posterior teeth.

The dorsal scutes of *Belodon* are much more strongly carinated than those of *Stagonolepis*. Whether *Belodon* possessed ventral scutes or not, is not certainly known; but I find no scutes which can be certainly recognised as such among Von Mayer's numerous figures.

The *Crocodilia* are definable from all other *Reptilia*, recent and extinct, by the following osteological characters:—

The majority of the cervical and thoracic vertebræ have transverse processes which are divided into more or less distinct capitular and tubercular portions; and the proximal ends of the ribs which appertain to these vertebræ are divided into capitula and tubercula. The dorsal ends of the sub-vertebral caudal bones are not united. The quadrate bone is immoveably fixed to the sides of the skull. The pterygoid bones send forward processes which separate the palatines and reach the vomers. There is an interclavicle, but no clavicles. The ventral edge of the acetabular portion of the ilium is entire or notched. The ischia are not greatly prolonged backwards, and the pubes are directed forwards and inwards. The femur has no prominent inner trochanter. The astragalus is not a depressed and concavo-convex bone with an ascending process. There are, at fewest, two rows of dermal scutes, one on each side of the middle line of the dorsal region of the body.

Stagonolepis and *Belodon* come within the order *Crocodilia*, as thus defined, and constitute the first of three sub-orders distinguishable on purely anatomical grounds.[1]

SUB-ORDER I. *Parasuchia*.—Neither the palatine nor the pterygoid bones develope osseous plates which prolong the nasal passages and

[1] 'On *Stagonolepis Robertsoni* and on the Evolution of the Crocodilia.'—'Quarterly Journal of the Geological Society,' 1875.

give rise to secondary posterior nares. Consequently, the nasal chambers communicate with the mouth by apertures situated beneath the anterior part of the skull. The Eustachian passages are not inclosed by bone (*Belodon*). The centra of the vertebræ are amphicœlous. The coracoid is short and rounded. The ala of the ilium is high, with a large and projecting anterior dorsal angle; and its acetabular margin is entire, the middle portion projecting beyond the anterior and posterior extremities of that margin. The ischium is short dorso-ventrally, elongated longitudinally; and its acetabular portion resembles that of a Lizard. The characters of the manus and pes are unknown.

There are two longitudinal series of articulated carinated dorsal scutes; and in *Stagonolepis*, but apparently not in *Belodon*, there is a ventral thoraco-abdominal shield, formed of not more than eight longitudinal series of articulated flat scutes, each of which consists of only one piece of bone.

Genera, *Stagonolepis* and *Belodon*.

SUB-ORDER II. *Mesosuchia.*—The palatine bones give off osseous plates, which shut off nasal passages from the mouth; secondary posterior nares, which are situated beneath the middle or hinder part of the skull, are thus produced. The pterygoid bones take no share in the formation of this passage. A middle Eustachian canal is included between the basi-occipital and the basi-sphenoid, but the lateral canals are represented only by grooves. The centra of the vertebræ are amphicœlous.

The coracoid is elongated. The ala of the ilium is lower than in the preceding, higher than in the following sub-order, and has, at most, only a slight prolongation of its antero-dorsal angle. The acetabular margin is nearly straight; and hardly, if at all, excavated. The ischium is more elongated dorso-ventrally, and shorter antero-posteriorly, than in the *Parasuchia*. Its acetabular margin is excavated by a notch, which marks off a stout pubic process, as in the next division. The manus and pes are constructed as in the next sub-order.[1]

[1] The manus is usually imperfect in even the best preserved fossil *Crocodilia*, but D'Alton and Burmeister ("Der Fossile Gavial von Boll," 1854) have figured and given Fitzingers' description, with additions of their own, of a nearly complete manus of *Pelagosaurus Bollensis* (Upper Lias) in the Vienna Museum. In all essential respects, the structure is identical with that of the manus of the *Eusuchia*, even down to the absence of claws on the terminal phalanges of the fourth and fifth digits, and the relative brevity and thickness of the first metacarpal. The same authors have shown that the pes of this oldest known form of the

There are two longitudinal series of dorsal scutes, more or fewer of which are carinated; and, in most of, if not in all, the members of this division, there is a ventral thoraco-abdominal shield composed of not more than eight longitudinal series of flat scutes, each consisting of a single piece of bone. (See Plates XI. and XII. [Plates 18, 19)].

To this division belong the genera *Steneosaurus*, *Pelagosaurus*, *Teleosaurus*, *Teleidosaurus*, and *Metriorhynchus;* with, probably, *Goniopholis*, and *Pholidosaurus*.

SUB-ORDER III. *Eusuchia*.—Both the palatine and the pterygoid bones are produced into osseous plates, which prolong the nasal passages backwards, and give rise to secondary posterior nares situated beneath the hinder part of the skull. There is either a central Eustachian canal, with two lateral grooves; or, more usually, there are three canals, completely enclosed by bone. The centra of the vertebræ which succeed the atlas and axis are procœlous, except in the case of the sacral and the first caudal, which last is doubly convex. The coracoid is elongated. The ala of the ilium is so low, in front, as to be almost obsolete, and there is only a rudiment of an anterodorsal process. The acetabular margin has a well-marked notch. The ischium is elongated dorso-ventrally and short antero-posteriorly. The acetabular margin presents a deep excavation, in front of which is a strong process, with which the pubis is articulated.

The number of the digits is five in the fore foot, and four, with a rudimentary fifth, in the hind foot.

There are always more than two longitudinal series of carinated dorsal scutes, and always more than eight series of flat ventral scutes, when the latter are present. The ventral scutes are made up of two ossifications, united suturally. (See Plate XIII. [Plate 20].)

It is obvious, from the mere statement of the characters of these three divisions, that the one which I have termed *Mesosuchia* is intermediate between the other two. It is further obvious that the *Parasuchia*, in those respects in which they differ from the *Mesosuchia*, approach the *Ornithoscelida* and the *Lacertilia*, especially such *Lacertilia* with amphicœlous vertebral centra as the existing *Sphenodon*, and the extinct *Hyperodapedon*. In fact, I know of no reptiles the skull and pectoral arch of which so nearly approach the structure

Mesosuchia, no less closely resembled that of the *Eusuchia*. The Memoirs of MM. Deslongchamps, father and son, contain an admirable account of the organisation of the *Mesosuchia* at present known. See the 'Prodrome des Téléosauriens du Calvados,' in the 'Notes paléontologiques,' vol. i., by M. Eugène E. Deslongchamps, and the various memoirs of M. Eudes Deslongchamps, contained in the 'Bulletin' and the 'Mémoires of the Société Linnéene de Normandie.'

found in *Belodon* and *Stagonolepis*, as they do in *Sphenodon*. (See Plate IX. [Plate 16].)

On the other hand, the *Eusuchia* are those *Crocodilia* which depart most widely from the Lacertilian type and are the most completely specialised Crocodiles.

The differences between the *Mesosuchia* and the *Eusuchia* are of no great moment. The Messrs. Deslongchamps, in their 'Prodrome des Téléosauriens du Calvados' ('Notes Paléontologiques,' Vol. I. 1863–9) have shown that the secondary posterior nares of *Metriorhynchus*, which ranges from the Kelloway rock to the Kimmeridge clay, are situated further back than those of *Pelagosaurus*, which is confined to the Upper Lias. Let this process be carried a little further by the union of the pterygoids; let the posterior faces of the centra of the vertebræ become slightly convex, instead of being, as at present, slightly concave; and *Metriorhynchus* would afford a complete transition from the *Mesosuchia* to the *Eusuchia*.

The *Parasuchia*, in the position of the anterior nares; in the absence of secondary posterior nares, and of Eustachian canals enclosed by bone; in the rounded form of the coracoid; in the configuration of the ilium and the ischium; depart more widely from the *Mesosuchia* than the latter do from the *Eusuchia*.

From a purely morphological point of view then, the three subdivisions of the *Crocodilia* form a series, slightly interrupted between the *Mesosuchia*, and the *Eusuchia*, but with a larger gap between the *Mesosuchia* and the *Parasuchia*. But, whatever the value of this break between the three terms of this series, this much is clear, that the modifications of structure needful to connect one with the other are of the simplest kind and are throughout of the same order. The kind of change which would convert a Parasuchian into a Mesosuchian, would, if continued, convert a Mesosuchian into an Eusuchian.

Hence, if there is any solid historical foundation for the doctrine of Evolution, the *Eusuchia* ought to have been developed from the *Mesosuchia*, and these from the *Parasuchia*; and if this process of evolution has taken place under such conditions that the skeletons of the *Crocodilia* which have existed during its occurrence have been preserved, geological evidence should prove that the *Parasuchia* have preceded the *Mesosuchia*, and that the *Eusuchia* have succeeded them in order of time.

Now this is exactly what the geological evidence does prove. It is established that these reptiles occur in the following stratigraphical order:—

1. The *Parasuchia*, in the - - *Trias* and perhaps earlier.
2. The *Mesosuchia*, in the Middle Mesozoic rocks from the *Upper Lias* to the *Wealden.*
3. The *Eusuchia*, in the later Mesozoic rocks and in the Tertiaries from the *Later Cretaceous* to the *Recent Epoch.*

In other words, the order of occurrence of the three divisions of the *Crocodilia* in time, coincides with the order in which they depart from the Lacertilian type, and put on special crocodilian characters ; and thus, palæontological fact is in precise accordance with the needs of the theory of Evolution. The evidence in favour of the gradual development of existing from ancient *Crocodilia*, is in fact as cogent, though not so complete, as that by which the origin of the horse from a three-toed ancestor has been demonstrated.

The evolution of *Equus* from its anchitherioid ancestor appears to have nearly occupied the time represented by the Miocene deposits ; while the evolution of the Eusuchian from the Parasuchian Crocodiles seems to have nearly coincided with the time represented by the deposit of the Jurassic formations.

It is very hard to estimate the amount of evolutionary work done in the change of one form into another, in widely different groups of the animal kingdom ; but perhaps it will not be very far from the truth, to regard the one set of changes as about equal in value to the other.

Admitting the origin of the Horse by a process of gradual modification from some tridactyle or tetradactyle Eocene ungulate mammal, we cannot rest there. This Eocene form must have proceeded from some pentadactyle ungulate mammal, which must have existed before the Tertiary epoch, if it be true, as is commonly believed, that all the oldest known Eocene *Ungulata* possess not even a rudiment of the first digit.[1]

By a parity of reasoning, the ancestors of the *Parasuchia* must be sought in the older Triassic deposits, or in formations of still earlier date ; and I think that it is not difficult to form a probable hypothesis as to the general characters of these ancestral forms, which in Haeckel's nomenclature would be termed *Prosuchia.*

The oldest *Crocodilia* known are, as I have shown, distinguished from the more recent forms by less divergence from such *Lacertilia* as *Sphenodon*, the type of the *Rhynchocephala* of Günther. We are

[1] According to the recent observations of Prof. Marsh. *Coryphodon* has five digits.

therefore warranted in assuming that, in the immediate ancestors of the *Parasuchia*, the fundamental differences from the *Lacertilia* were still further lessened; that, in other words, the *Prosuchia* were intermediate between *Parasuchia* and *Lacertilia*, in the same way as the *Mesosuchia* are intermediate between *Parasuchia* and *Eusuchia*.

II.—A DENTIGEROUS BONE, INCERTÆ SEDIS.
(PLATE IV. [PLATE 11] FIG. I.)

In my first paper on *Stagonolepis*, I have described "the impression of a fragment of what I conceive to be the lower jaw, exhibiting the remains of some eight or nine alveoli." After describing this impression I go on to observe—

"There is no positive proof that this fragment of a jaw belonged to *Stagonolepis;* but, as I have already stated, no vertebrate remains save those of this reptile have hitherto been found in the Findrassie quarry, whence this specimen was obtained, and the external characters and mode of implantation of the teeth are wholly unlike those of any of the large, probably piscine teeth (of *Dendrodus*, *e.g.*) which have been discovered in the neighbouring beds of the Old Red Sandstone . . . . If this jaw belonged to the same animal as that to which even the largest of the vertebræ which have been discovered belonged, the size of the teeth is remarkable, for the longest is considerably more than twice as long as the centrum of such a vertebra. On the other hand, it must be recollected that the teeth of the ancient *Teleosaurus* are extremely long in proportion to the jaw, and, in other respects, present resemblances to those contained in the fragment just described; while it is also possible that this fragment may have formed a part of an individual larger than any of those whose vertebræ have, as yet, come to light. As the evidence stands, at present, I see no reason to doubt that the jaw belonged to *Stagonolepis*."

By degrees, however, the materials which have come into my hands proved that the latter conclusion was untenable; and, two years ago,[1] I expressed the conviction that "the mandible with long curved teeth, which I supposed might belong to *Stagonolepis*, certainly appertains to some other animal."

I have since carefully re-examined this impression, the drawing of a cast of which is given in Plate IV. [Plate 11] fig. 1.

The structure of which this impression alone exists, has evidently been a fragment of a crushed and mutilated bone which bore four

[1] 'On *Stagonolepis Robertsoni*, and on the Evolution of the Crocodilia.'—'Quarterly Journal of the Geological Society,' vol. xxxi., p. 424.

teeth. The bone, opposite to that edge on which the teeth are set, is obviously imperfect, and its two ends are broken.

The total length of the fragment is 6·5 inches. The surface impressed by the bony matter is irregular, and has a peculiar vertical striation, as if the bone had possessed a coarsely fibrous structure. Moreover, the alveolar edge is very irregular.

The most anterior of the four teeth is situated at one extremity of the bone. Between the anterior contour of its fang and the posterior contour of the fourth tooth is a distance of four inches.

The first tooth is the slenderest. It has a slight curvature, the anterior face being more curved than the posterior. The second tooth is broader, straighter, more acutely pointed, and is the shortest of all. The third is the longest and stoutest as well as the most curved ; and its impression, which is incomplete at the apex, projects 2·25 inches beyond the alveolar margin of the jaw. The base of the tooth is rather more than half an inch thick. The hindermost tooth is inclined backwards, and has evidently been much crushed before, or during, its enclosure in the sandstone matrix.

In my first paper, I have spoken of the alveoli of this fragment of a jaw ; and no doubt there are appearances which lend themselves to the view that the teeth were lodged in alveoli, and that empty alveoli existed in the space between the third and fourth, and behind the latter tooth ; and, possibly, between the second and third teeth. But it is impossible to make sure of their existence, and I would rather leave that point open.

The impression of each tooth is marked by raised longitudinal striæ, which are obviously casts of grooves on the face of the tooth. They are irregular at the base, nearly parallel in the middle, and die out towards the apex of the tooth, which is nearly smooth.

The bases of the teeth do not expand where they join the bony substance of the jaw, and the manner in which they have been crushed strongly suggests the existence of a large pulp cavity. On the other hand, it may be that the longitudinal striæ indicate true longitudinal grooves of the face of the tooth, and not fractures ; and that the crushing of the bases of the teeth, like the splintery aspect of the substance of the bone, may be due to pressure, subsequent to fossilization.

Nothing is to be seen of any impressions of small teeth, between the large ones.

Looking at the texture of the bone and the longitudinal groovings of the teeth (if the ridges really express natural grooves), one would be inclined to refer this fossil either to the Labyrinthodonts, or to such a fish as *Rhizodus*.

On the other hand, the absence of small teeth, and of any clear indications of ankylosis of the teeth to the jaw, no less than the presence of large pulp cavities (if the mode in which the teeth are fractured may safely be taken as indications of these), point to affinities with such reptiles as *Megalosaurus*.

The impression of the bony substance of this jaw alone is sufficient to exclude any comparision with *Stagonolepis*, the texture of the osseous matter of the mandibles and maxillæ in that reptile being remarkably close and dense.

As it may be convenient that the animal to which this jaw belonged should have a name, I will call it *Dasygnathus longidens*.

III.—THE ICHNITES OF THE CUMMINGSTONE SANDSTONES

In the year 1851, Captain Lambert Brickenden gave the following account[1] of a series of footmarks which he had discovered in a quarry of the sandstones of Cummingstone, near Elgin.

"The slab exhibits on the surface, in a very striking manner, thirty-four footprints of a quadruped, traced in an uninterrupted succession across the stone. The impressions of the right feet alternate with those of the left, from which they are separated laterally by an interval of 3 inches, the length of each stride or pace being about 4 inches. The imprints of the fore and those of the hind feet are nearly in contact, and bear a precisely similar relation throughout, the size of the footmarks in the former in proportion to the latter is as three to four, the hinder being about 1 inch in diameter.

"The imprints are slight cavities, and are all characterised by the same rounded and blunt appearance, apparently indicating that the articulations of the feet were closely connected, although, from the crystalline and arenaceous surface of the stone, the form and number of the joints of the toes cannot be positively determined.

"A slight trailing mark is observable between the footmarks. In some of the marks it appears that the foot, in pressing in the originally yielding sand, had slightly raised the surface of the heel, but this is scarcely perceptible in the drawing."

The track is figured of one-sixth of the size of nature in the plate which accompanies the paper.

Various slabs of sandstone from the Cummingstone quarries, exhibiting footmarks, were sent to me in 1858, and I have figured and

[1] 'Quarterly Journal of the Geological Society,' 1852, vol. viii., p. 98.

described some of these imprints in my first Memoir on *Stagonolepis*. No new materials of importance have since come into my hands, but some additional experience in dealing with tracks has led me to doubt whether my interpretation of the impressions in question was in all respects correct. Those who have studied such markings most carefully will be the readiest to acknowledge the extreme difficulty of arriving at a definite conclusion as to the cause of appearances, which vary, not only according to the softness or hardness of the sand on which the animal walked, but exhibit the most astonishing differences when lighted from different sides.

The most complete impressions I have seen (Plate XIV. [Plate 21]) form part of a series of three pairs of right, and two pairs of left footprints. The former measure about 2 feet 6 inches from the hinder end of the hind foot to the front end of the fore foot of the same side. The distance between the median edges of the two sets of footprints nowhere exceeds 4 inches. The stride, or distance between corresponding points of successive impressions of the same foot, is, as nearly as may be, 12 inches; and the long axes of the pedal impressions are nearly parallel with the line of march, the marks of the digits being only very slightly convex inwards.

The impressions of the two feet, which constitute a pair of the same side, are close together, the anterior extremity of the posterior impression just reaching the posterior margin of the anterior impression. The centre of the posterior impression is a little external to that of the anterior impression, so that the outer margin of the former projects beyond that of the latter. There is no sign of any trail between the right and left set of footmarks.

These characters of the tracks, taken together with the dimensions of the footmarks, appear to me to indicate that the animal which made them possessed limbs, which were long relatively to the transverse diameter of its body, and which moved in a plane nearly parallel with the median longitudinal plane of the body. The footprints which are best defined are the hinder and the middle pair on the right side; but the hinder pair have been made upon a part of the sand which was firm, while the middle pair have fallen upon a soft wet place, whence the feet have sunk deeper and a thick ridge of sand has been thrown up behind each. Hence the two pairs of impressions must be taken together in judging of the form of the foot which gave rise to them. The posterior pair furnish the best guide to the actual size of the feet, while the anterior pair give the better insight into some points of their structure.

The posterior pair of impressions are represented in Plate XV. [Plate 22] fig. 5.

The forefoot presents a convex posterior margin, in front of which is a smooth space, indicating a half-moon shaped pad in the sole of the foot. In front of this, are seen three sharp and well-defined longitudinal groove-like depressions, as if of as many digits sheathed in claws. The two longitudinal depressions on the inner side of the foot are of nearly equal length and strength ; while the outer is shorter, not so well-marked, and more distant from either of the two long grooves, than they are from one another. The impression of the sole projects for some little distance on the outer side, beyond the short groove ; as it does on the inner side, beyond the innermost of the long grooves.

On comparing this with the front footmark of the middle pair (Plate XIV., *B* [Plate 21]), which was certainly made by the same foot, the difference between the two appears at first sight very considerable, and especially does the impression (*B*) seem to be that of a much broader foot. Nevertheless, if the two longer longitudinal grooves in the imprint last described be compared with the strong longitudinal grooves in that represented in Plate XV. [Plate 22] fig. 1, they will be found to correspond very closely in size, form, and distance from one another, while a fainter and shorter longitudinal marking lies on the outer side of the foot, at the same greater interval from the two long impressions, as in the foregoing case. Moreover, there is a similar projection of the sole on the outer side beyond the short impressions. In addition, the middle footmark (*B*) shows another longitudinal marking, faint in front, but becoming deeper behind, which lies parallel with the inner of the two longest longitudinal grooves already mentioned. Beyond this, the impression of the sole extends a little way, and from its inner end a still more faint longitudinal mark extends forwards, and ends at about the level of the hinder extremities of the two longest and strongest longitudinal grooves. A well-marked transverse groove, deeper and wider at its inner than at its outer end, and hence, when lighted obliquely, having the aspect of a comma, marks the place at which the shelving posterior part of the impression of the sole ends. In some lights, the form of the impressed surface in this region is such as to give rise to the appearance of an inwardly directed thumblike digit, such as I have mentioned in my first paper, but I am now convinced that the facts do not warrant this interpretation.

The interspaces between the longitudinal depressions are convex and smooth, as if they had been moulded by a web, and a tolerably well-defined line, concave forwards, which lies between the innermost and the second longitudinal depression, marks, I conceive the anterior boundary of the web in this region.

It can hardly be doubted, I think, that the longitudinal depressions indicate as many digits. In this case, the animal must have possessed a broad forefoot, provided with five, probably clawed, toes, of which the three middle were much longer than the inner and outer; and these digits were, in all probability, connected by webs.

The greatest length of these footmarks, judging from the posterior one, in which the hinder margin is best defined, is 3·5 inches, while the width can hardly have been less than 3 inches, and may have exceeded this dimension.

The impression of the hinder foot, in its general character, is very similar to that of the forefoot, but the toes are shorter relatively to the sole. The marks of four digits are plainly discernible, and there are indications of interdigital membranes between them. I am not quite certain as to the existence of a fifth toe. I do not think that the transverse diameter can have exceeded 2·5 inches, nor the antero-posterior diameter have quite reached that length.

The excess of size of the anterior over the posterior footmarks is a very striking peculiarity of these tracks. I do not think there can be any doubt that the posterior footmarks belong to the hinder feet. Not only are they regularly posterior in position; but, in the middle pair of the right side, figured in Plate XIV. [Plate 21], the straight markings which indicate the digits of the hinder impression encroach upon the disturbed sand behind the anterior footmark, in such a way as to show that they must have been made after the anterior impression was formed; or, in other words, by a foot which was put down after the forefoot had been taken away.

On one side of the slab, near the middle pair of footprints of the track just described, are two confused marks of similar feet, but fully twice as large (Plate XV. [Plate 22] fig. 6).

Plate XVI. [Plate 23] represents, on a reduced scale, the surface of another slab of sandstone from Cummingstone, about 3 feet long by 20 inches wide, covered with tracks of quadrupedal animals, which all appear to have been going the same way, as if a herd were travelling together.

The footprints (some of which exceed 1·5 in. in transverse diameter) alternate, and those of the fore and hind feet are close together; the right and left series being separated by an interval which is narrow in proportion to the breadth of the foot, as in the preceding tracks. Moreover, they resemble the larger footprints in their width relatively to their length, and in the rounded posterior contours of the impressions. They differ in the relatively smaller size of the anterior footprints.

In some of these tracks the anterior impressions appear to be smaller than the posterior (Plate XV. [Plate 22] figs. 1 and 4); and in some, it looks as if the fore foot had only three digits, while the hind foot had four. (Plate XV. [Plate 22] fig. 4.)

The two sets of footsteps here described agree with those discovered by Captain Brickenden, in their rounded posterior contours, in the alternation of the pairs of opposite sides, and in the direction of the long axes of the feet parallel with the line of march. They differ, not merely in absolute size, but in the distance between the two series of tracks made by the same animal, relatively to the size of the footprints; and, still more remarkably, in the relative sizes of the fore and hind footprints, the first-described set alone having the anterior footprints the larger.

On comparing these ichnites with others, the Triassic *Cheirotherium* is obviously excluded, as are the singular footprints from Shrewley Common described by Murchison and Strickland;[1] nor, among the numerous figures and descriptions[2] of footprints which I have examined, do I find any which closely approach these, except some of those from Dumfriesshire, which have been the subject of Memoirs by Dr. Duncan,[3] Sir W. Jardine,[4] and Mr. Patrick Dudgeon.[5]

The impressions described by Dr. Duncan have the general facies of those here described, but the impressions of the fore and hind feet are said to be nearly equal. In Sir William Jardine's work, the figures of footprints which come nearest to the first described set from Cummingstone, are to be found in Plate VI. [Plate 13] and Plate XI. [Plate 18] (*Chelichnus ambiguus*), and Plate XIII. [Plate 20] (*Batrachichnus Lyellii*). But, in both these, the anterior footmarks are the smaller.

Without wishing to express any opinion as to the actual affinities of the makers of the various kinds of footprints, I think it will be convenient to consider the first series of footprints which are here described as a modification of Sir W. Jardine's *Chelichnus*, and to name them *Chelichnus megacheirus*. The second series of tracks are not sufficiently well marked to justify the application of any specific name to them.

[1] 'On the Upper Formations of the New Red Sandstone System.'—'Transactions of the Geological Society of London,' Se. II., vol. v., 1857.

[2] In Hitchcock's 'Ichnology of New England,' and its supplemental volume, for example, I find no track but 'Shepardia' in Plate XXIV., fig. 2, of the first-mentioned volume, which, even remotely, approaches *Chelichnus*.

[3] 'An Account of the Tracks and Footmarks of Animals found impressed in Sandstone in the Quarry of Corncockle Mine in Dumfriesshire.'—'Transactions of the Royal Society of Edinburgh,' vol. xi., 1828.

[4] 'The Ichnology of Annandale,' 1853.

[5] 'Proceedings of the Royal Society of Edinburgh,' vol. ix., p. 154, 1876.

The questions of the nature of the animals which gave rise to *Chelichnus* tracks, and of the relations of such animals with *Stagonolepis*, appear to me, at present, hardly to admit of profitable discussion, except so far as certain negative conclusions may be pretty safely reached.

Footprints, similar to those which I have named *Chelichnus megacheirus*, could not have been made by any existing species of Crocodile, nor by any of the *Mesosuchia*, if we may draw a general conclusion respecting the structure of the feet of these reptiles as a whole, from those in which the structure of the feet is accurately known.

In all recent Crocodiles, the pentadactyle fore foot is considerably smaller than the tetradactyle hind foot. In the fore foot, the second and third digits are nearly equal in length, and are directed forwards, in the standing or walking attitude; the first digit is much shorter, and turns a little inwards; the fourth, also much shorter than the third, is inclined obliquely outwards, while the still shorter and weaker fifth digit often stands at a right angle to the long axis of the foot, or may even be inclined backwards.

In the hind foot, the second and third digits are longest and equal, as in the fore foot. The hallux and the fourth digit are also of nearly the same length and much shorter than the middle toe. The hallux lies nearly parallel with the second digit, but the fourth toe diverges outwards to a certain extent.

It is obvious that feet such as those just described could not, by any possibility, give rise to such impressions as those of *Chelichnus megacheirus*.

At the same time, the large size of the distal end of the humerus relatively to that of the femur in *Stagonolepis*, and the great thickness of the metatarsal or metacarpal bone (Plate VIII. [Plate 15] fig. 5), suggest that the *Parasuchia* may have had larger fore feet and broader metacarpal and metatarsal regions than the *Mesosuchia* and *Eusuchia;* while it is, at any rate, not improbable, that, to the many approximations of the *Parasuchia* to the *Lacertilia*, there may have been added a complete fifth toe on the hind foot.

Leaving aside the Geckos and the Chamæleons, which hardly need to be considered in the present comparison, the fore and hind feet of the Lizards present a very general and characteristic uniformity. Both are pentadactyle, and the fore foot is smaller, usually much smaller, than the hind foot.

In the fore foot, the fourth digit is the longest and may be directed almost or quite forwards, *i.e.*, in the line of march. The fifth digit is

much shorter, and the other digits gradually decrease in length, from the third to the first. Thus, the imprints of such a foot will contain the marks of a long digit, on the inner side of which diverge three shorter digits, and on the outer side, one.

In the hind foot, the fourth digit is also longest, but it is directed obliquely outwards, and the first three digits, successively shorter from the third to the hallux, lie on its inner side, the hallux being nearly parallel with the line of march. The fifth toe is well separated from the fourth, on the outer side of the foot, and projects outwards at right angles to the long axis of the foot, or even more or less backwards.

If the ancient Lizards of the Trias possessed feet similar to those of modern Lizards, and all that is known of *Telerpeton* and *Hyperodapedon* leads to the conclusion that they did, it is clear that they can have had nothing to do with the production of *Chelichnus* tracks.

Dr. Buckland suggested that the Dumfries footmarks were made by Chelonians, and this conclusion has been accepted by Professor Owen, who went so far as to name the particular tortoise which left the tracks, *Testudo Duncani*.[1]

In the Tortoises which I have had an opportunity of examining, the disposition of the digits of the fore and hind feet, and the marks which they leave when the animal walks are very characteristic. In the fore foot, the majority of the five toes are turned inwards, in such a manner that their apices describe a curve, the convexity of which is turned inwards. In the hind foot, on the contrary, the toes are turned outwards, and their apices occupy a curve, the convexity of which is turned outwards and forwards. Thus, for the feet of the same side, the curves are nearly at right angles to one another.

The fore and hind feet have nearly the same dimensions in the Tortoises. The nail marks on the imprints of the feet are short relatively to the impressions of the broad palmar or plantar pad. The hind foot generally drags, scraping a long broad mark as it is thrown forwards. In walking, it is usually set down in the imprint of the fore foot, which it more or less obliterates. Sometimes, however, the hind foot oversteps the impression of the fore foot of the same side, so that the hind footprint may lie in front of the fore footprint.

In their brevity, breadth, and short claw marks, the imprints of

[1] "Report on British Fossil Reptiles." Report of the eleventh meeting of the British Association for the Advancement of Science, p. 190.

tortoises' feet are somewhat like *Chelichnus;* but, in the latter, the characteristic inward twist of the anterior digits and outward twist of the posterior digits is wanting. At the same time, the breadth of the track, or the interspace between the right and left footprints, made by the same animal, in the Chelonians, is, in proportion to the size of the feet and the length of the stride, vastly greater than in *Chelichnus.*

In fact, there is really no ground for ascribing these tracks to Chelonians.

Living *Amphibia* never possess more than four complete toes on the fore feet, though most have five on the hind foot. The hind foot is usually the larger, though there is a great variation in this respect; and in *Urodela* (*e.g.*, *Menopoma*) there may be little difference between the two.

It is a very general rule that, as in Lizards, the fourth toe (apparent third in the manus) is the longest, in both the fore and the hind limbs. And the fourth toe is that which generally lies parallel with the direction of the line of march. This is particularly obvious in the pes of the *Anura*, where this toe, instead of being strongly bent outwards, as in the Lizards, is straight, or even slightly bent inwards. In the hind foot, the hallux is short, and is directed transversely inwards or even a little backwards. The imprint of this foot, therefore, is the reverse of that of the Lizards, inasmuch as the transversely directed toe is on the inner side of the foot, and not on its outer side.

I know of no Amphibian with feet such as could produce *Chelichnus* tracks.

The general result of these considerations is to lead me to doubt whether the *Chelichnus* tracks can, at present, be safely referred to any known form of Reptile or Amphibian. The tenor of the evidence appears to be strongly against ascribing them either to *Amphibia*, *Lacertilia*, or *Chelonia;* but I think it must be allowed that they might have been produced by pentadactyle *Parasuchia* or *Ornithoscelida.*

I am indebted to the Rev. Dr. Gordon for the following note upon the geological structure of the Elgin district, and for the valuable map showing the localities in which reptilian remains [Plate 24] and tracks occur, which accompanies this memoir.

NOTE UPON THE GEOLOGICAL STRUCTURE OF THE ELGIN DISTRICT, BY THE REV. GEORGE GORDON, D.D.

THE lower or northern part of Elginshire, in which reptiliferous beds appear, has been visited and described by several geologists. The different papers, containing the result of their observations, are referred to by Sir Roderick Murchison in the Quarterly Journal of the Geological Society for August 1859, and by J. W. Judd, Esq., in the same Journal for May 1873.

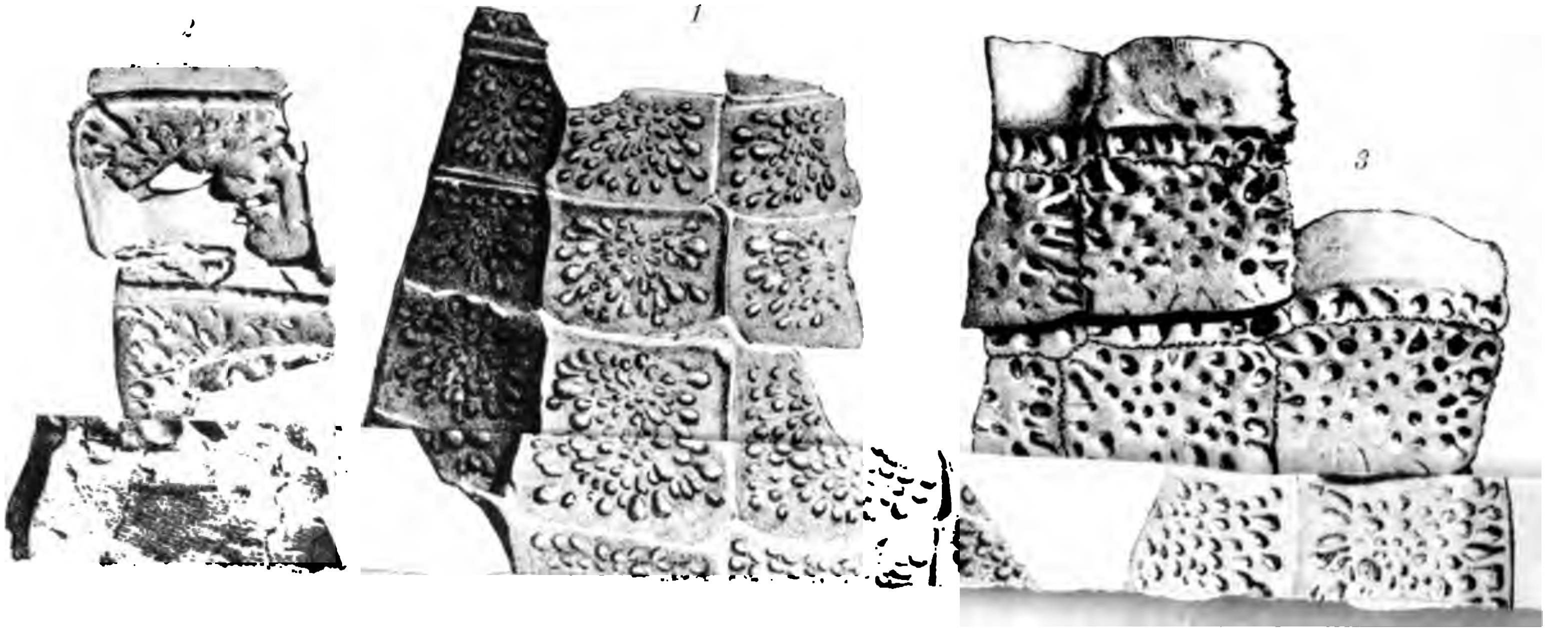
For some time after the discovery of the *Telerpeton*, at Spynie, and up to the finding of a slab at Findrassie, which clearly proved the reptilian character of *Stagonolepis*, these beds, conformably following, and lithologically resembling the holoptychian, or undoubted "Old Red" strata, were supposed to belong to the same geological epoch. The next discovery, of the *Hyperodapedon*, then induced most geologists to regard them as of a later, or the Triassic age.

Although the quarrymen are generally alive to any organism that may turn up in their labours, yet it is singular that no other remains (animal or vegetable) have as yet been detected in these reptiliferous beds; bones, scutes, and footprints forming the whole of their vestiges. There are concretions of pyrites, probably coprolites, but no organic structure has been seen in them.

The accompanying sketch [Plate 24] is intended to mark the different localities where the various rocks come to the surface, and to point out their dip, where it has been ascertained. No outline, to show their probable range, has been attempted.

The district is so covered by drift, that no junction of the holoptychian and reptiliferous strata has been laid bare.

It is supposed that the plain (of drift) on which Elgin stands, and particularly to the east of that town, is underlaid by the cherty or concretionary rock, and it again by the reptiliferous sandstones; but no vestige of reptilian remains has been found within this area.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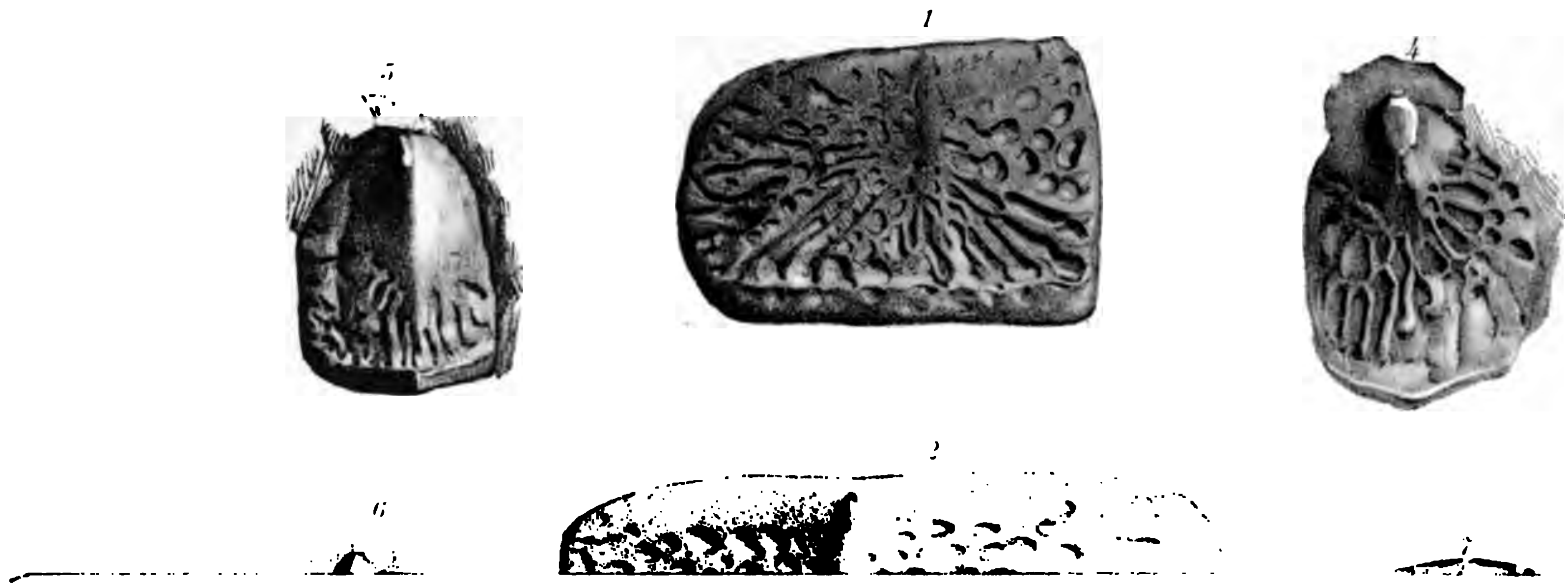

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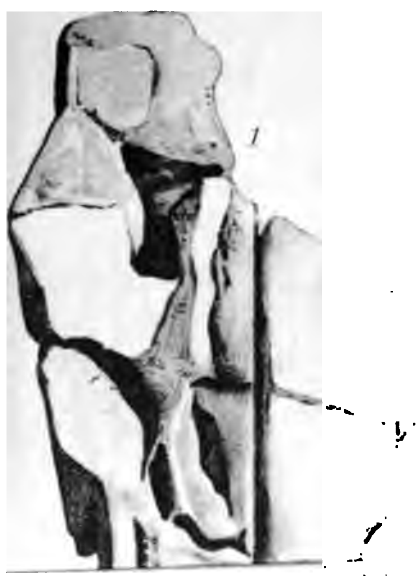
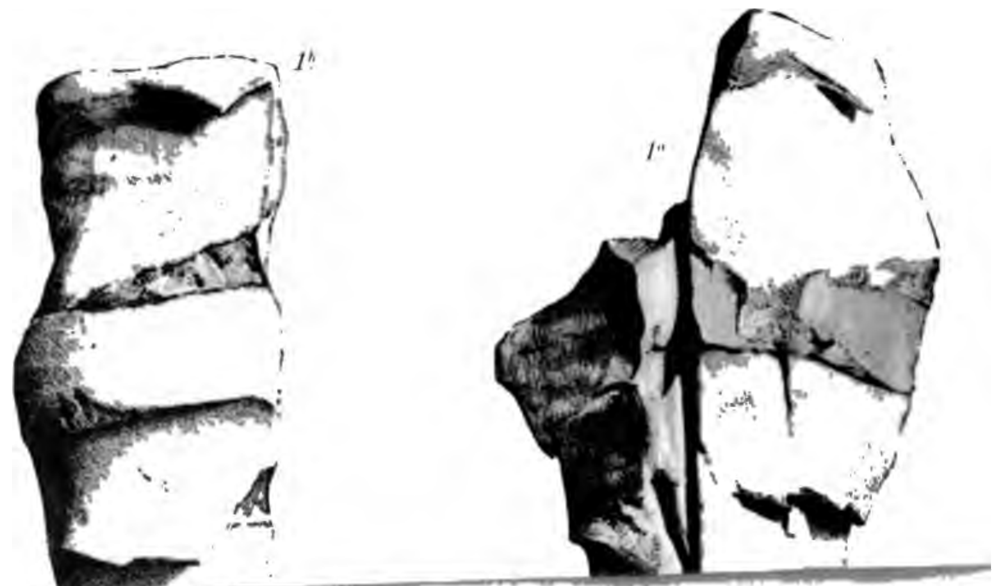


Plate III. in book.—Figs. 1, 1a, 1b, 1c, [illegible] natural size.
Fig. 2, natural size.



Scale for Fig. 2, [illegible] natural size.

DESCRIPTION OF THE PLATES.

PLATE I. [PLATE 8.]

Fig. 1. *Stagonolepis.*—The original specimen, exhibiting impressions of the ventral scutes described and figured by Agassiz: "Poissons fossiles du vieux Grès rouge," p. 139, and Plate XXXI. (Elgin Museum, No. 27.)

Fig. 1*a*. *Stagonolepis.*—A cast taken from the preceding specimen, exhibiting the characters of the pitted ornamentation of the original scutes.

Fig. 2. *Stagonolepis.*—Two ventral scutes. (Dr. Taylor's Collection.)

Fig. 3. Ventral scutes of a species of *Jacare*, showing the manner in which the successive zones overlap: the sutural union of the scutes of the same zone; that of the anterior and posterior portions of each scute; and the pitted sculpture of the exposed surfaces of the scutes.

Fig. 4. *Stagonolepis.*—Fragment of the upper and lower jaws, with teeth. (Museum of Practical Geology.)

Fig. 4*a*. The extremity of the mandible of the same specimen, showing a tooth in its alveolus. × 2.

Fig. 5. *Stagonolepis.*—Cast of an impression of the anterior end of a thoracic vertebra. (Elgin Museum, No, 36.)

Figs. 6, 6*a*, 6*b*. *Stagonolepis.*—End, lateral, and ventral views of the cast of an impression of a cervical vertebra. (Elgin Museum.)

Fig. 7. *Stagonolepis.*—End view of the cast of an impression of a posterior cervical vertebra. (Elgin Museum, No. 50.)

PLATE II. [PLATE 9.]

Fig. 1. *Stagonolepis.*—Cast of an impression of a dorsal scute. (Elgin Museum, No. 26.)

Figs. 2, 5, 6. *Stagonolepis.*—Cast of impressions of dorsal scutes on the same block of sandstone. (Elgin Museum, No. 2.)

Fig. 3. *Stagonolepis.*—The outer surface of a dorsal scute the bony matter of which is tolerably well preserved.

Fig. 4. *Stagonolepis.*—Cast of an impression of a dorsal scute. (Elgin Museum, No. 10.)

Fig. 7. *Stagonolepis.*—The impression of a ventral scute.

Figs. 8 and 9. *Stagonolepis.*—Impressions of the inner surface of a dorsal scute.

Fig. 10. *Stagonolepis.*—Inner face of a dorsal scute (from Lossiemouth), part of which has been cleared away to show the impression left by the outer surface.

Fig. 10*a*. A transverse section showing the angulation of this scute.

Fig. 10*b*. A sectional view of the outer extremity of the same scute.

PLATE III. [PLATE 10.]

Stagonolepis.—Fig. 1, ventral; Fig. 1*a*, dorsal; Fig. 1*b*, lateral aspect of the natural cast of a portion of the caudal region (in the Collection of J. Powrie, Esq.), two-thirds of the natural size. Fig. 1*c*, interior view of the longer half; and Fig. 2 the cast of the interior of the shorter half of the same fossil; of the natural size

R 2

PLATE IV. [PLATE 11.]

Fig. 1. *Dasygnathus longidens.*—Cast of the impression of the dentigerous bone. (Elgin Museum, No. 1.)

Fig. 2. *Stagonolepis.*—The cast of the impression of a caudal vertebra. (Elgin Museum, No. 4.)

Fig. 3. *Stagonolepis.*—The cast of the ventral aspect of the caudal fragment. (Plate III. fig. 1.)

Fig. 4. *Stagonolepis.*—The cast of the interior of the longer half of the same. (Plate III. fig. 1c.)

PLATE V. [PLATE 12.]

Figs. 1—1c. *Stagonolepis.*—The fragment of the skull with teeth described at pp. 21–23. (Elgin Museum, No. 38.)

Figs. 2—2b. *Stagonolepis.*—Anterior, lateral, and ventral views of the cast of an impression of a vertebra from the fore part of the thoracic region. (Elgin Museum, No. 22.)

Fig. 3. *Stagonolepis.*—Cast of an impression of the anterior end of a thoracic vertebra. (Elgin Museum, No. 11.)

Fig. 4. *Stagonolepis.*—Impression of the posterior end of the first sacral vertebra. (Elgin Museum, No. 47.)

Fig. 4a. Cast taken from the same specimen.

PLATE VI. [PLATE 13.]

Fig. 1. *Stagonolepis.*—The inner face of an ilium ; and

Fig. 2. A femur. Fig. 2a, contour of the exposed face of this bone. These two bones are represented of three-fourths the size of nature, and nearly in the relative position which they occupy on a block of Lossiemouth sandstone. (Elgin Museum, No. 46.)

Figs. 3—3c. *Stagonolepis.*—The imperfect symphysial end of a mandible with teeth. (Museum of Practical Geology.)

PLATE VII. [PLATE 14.]

Fig. 1. *Stagonolepis.*—The cast of an impression of a caudal vertebra.

Fig. 2. *Stagonolepis.*—The impression of the posterior face of a thoracic vertebra. (Elgin Museum, No. 12.)

Fig. 3. *Stagonolepis.*—The impression of the arch, and of the commencement of the spine, of a thoracic vertebra. (Elgin Museum, No. 49.)

Figs. 4, 4a. *Stagonolepis* (?)—Cast of an impression of a posterior caudal vertebra. (Elgin Museum, No. 17.)

Fig. 5. *Stagonolepis.*—A rib from Lossiemouth, one half natural size.

Fig. 6. *Stagonolepis.*—A cast of the impression of the vertebral end of a rib. (Elgin Museum, No. 26.)

Fig. 7. *Stagonolepis.*—Humerus. (Elgin Museum, No. 26.)

Fig. 8. *Stagonolepis.*—Femur. From Lossiemouth, one half natural size.

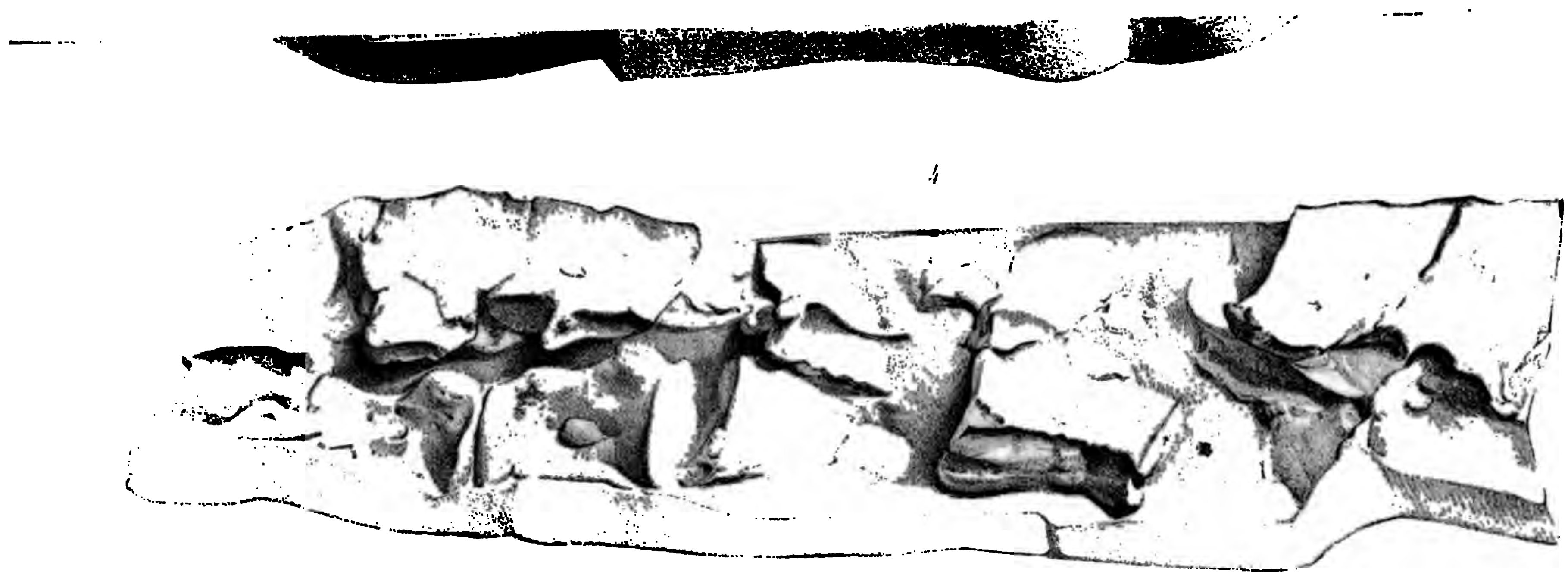
Fig. 9. *Stagonolepis.*—Radius or fibula. From Lossiemouth. (Elgin Museum, No. 33.)

PLATE VIII. [PLATE 15.]

Fig. 1. *Stagonolepis.*—Coracoid. From Lossiemouth. (Elgin Museum, No. 37.)

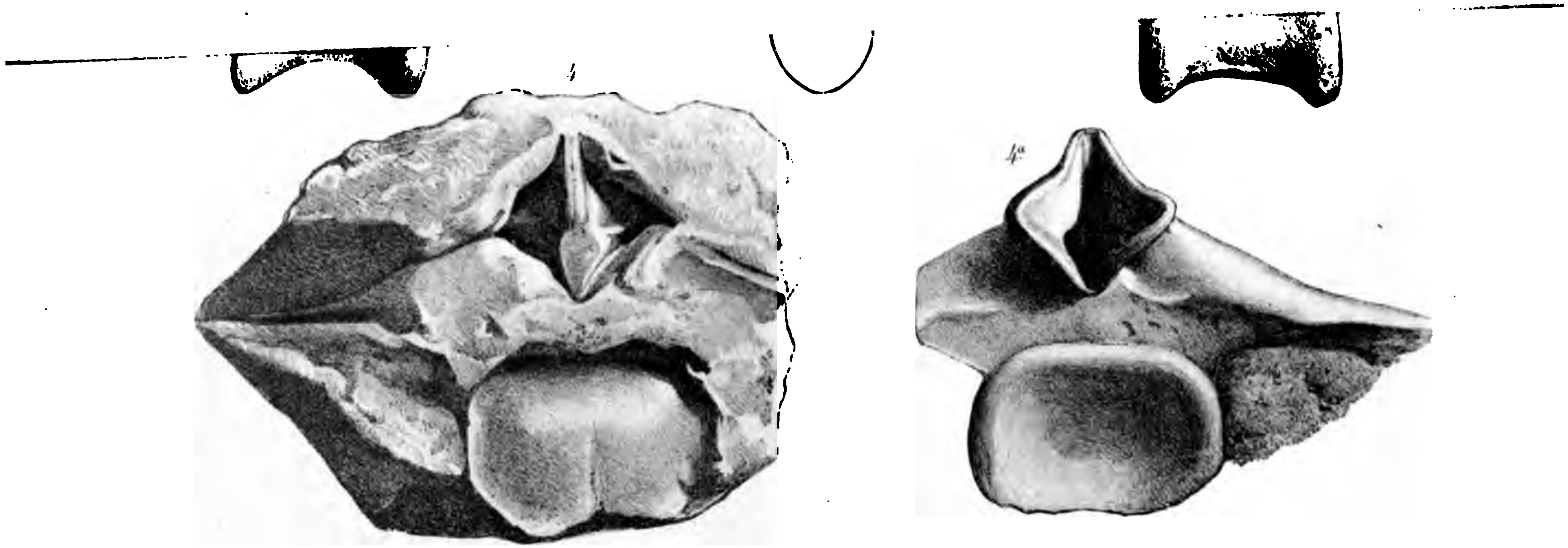
Fig. 2. *Stagonolepis.*—Pubis. From Lossiemouth. (Elgin Museum, No. 39.)

Figs. 3, 3a. *Stagonolepis.*—Cast of the impression of the inner face and posterior edge of a scapula. (Elgin Museum, No. 20.)



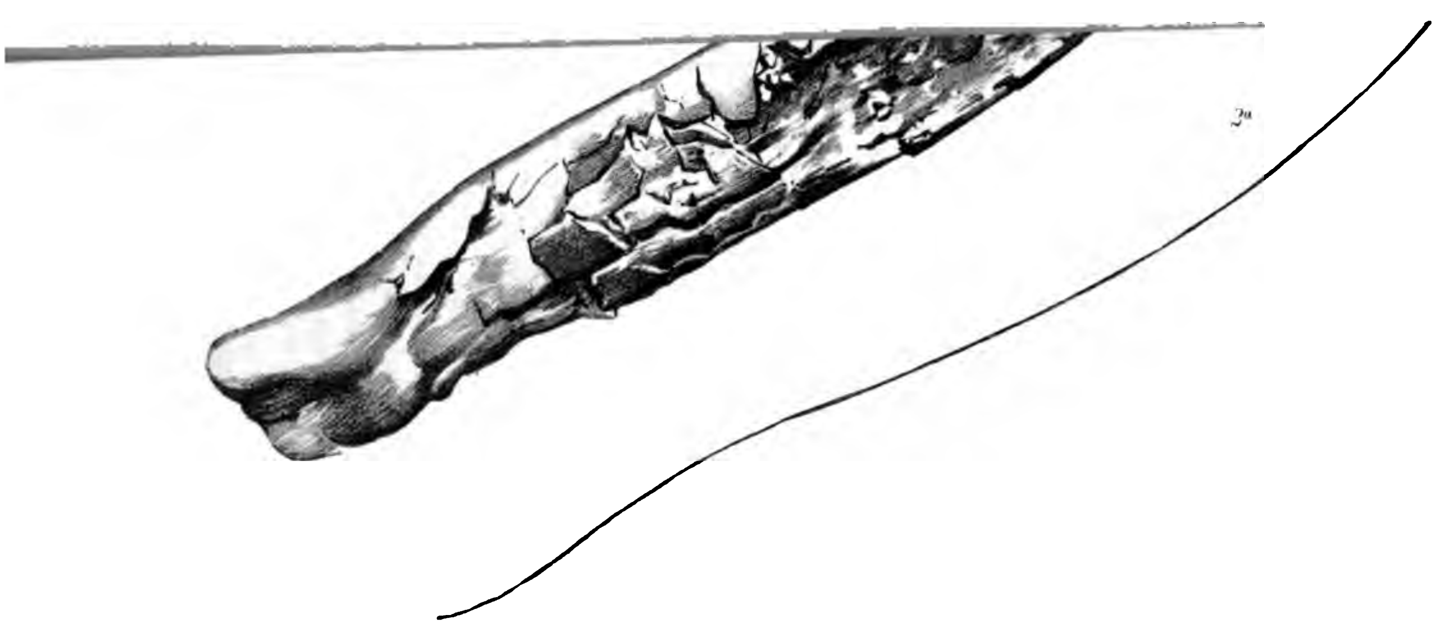
STAGONOLEPIS, FIGS. 2, 3, 4.

Scale—[illegible] size of Original Plate.



STAGONOLEPIS.

Scale–¼ size of Original Plate.



STAGONOLEPIS.

Scale $\frac{3}{4} \times \frac{6}{7} = \frac{9}{14}$ exact. ($\frac{9}{14}$ or) about $\frac{2}{3}$ natural size.

Plate VI. in book $\frac{1}{4}$ natural size.

STAGONOLEPIS.

Scale—½ size of Original Plate.

Geological Survey of the United Kingdom. [PLATE 15.] PLATE VIII.

STAGONOLEPIS.

Scale—½ size of Original Plate.

PLATE IX

Geological Survey of the United Kingdom.

[PLATE 16.]

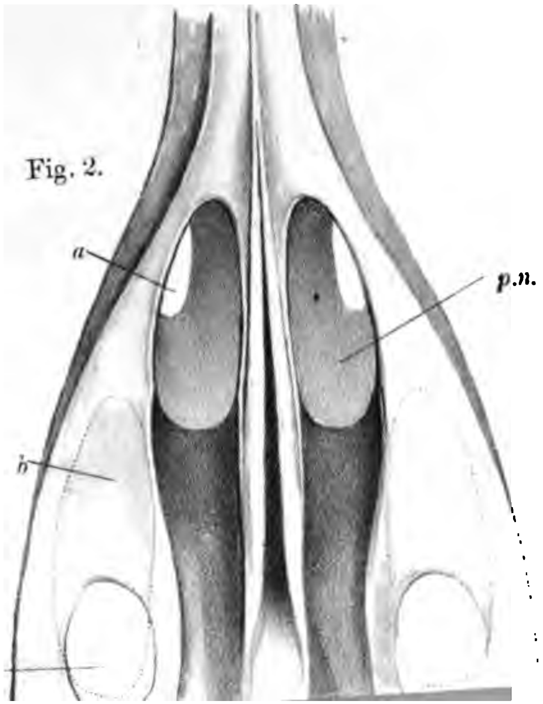


Fig. 2.

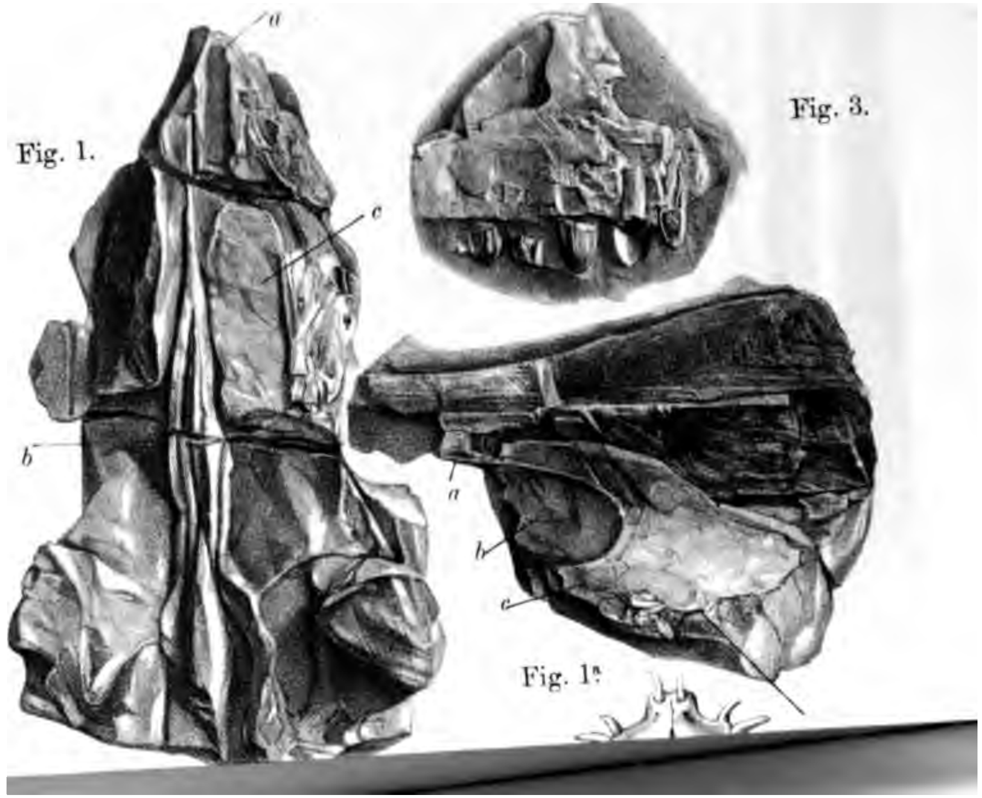


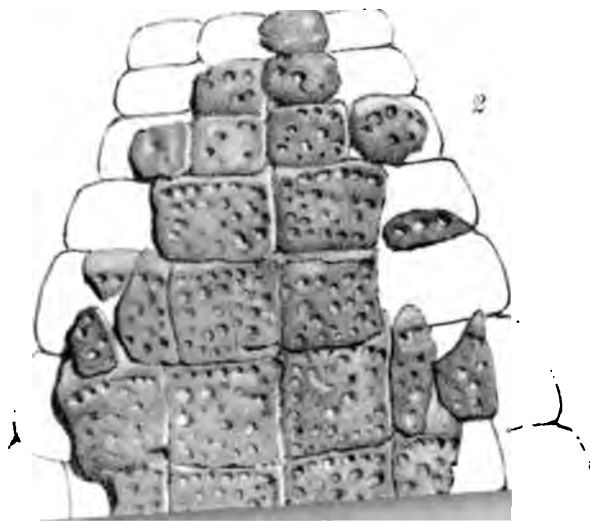
Fig. 1.
Fig. 3.
Fig. 1ª


1
1a
2
2a
3
5
5a

Plate XI.

[PLATE 18.]

Geological Survey of the United Kingdom.



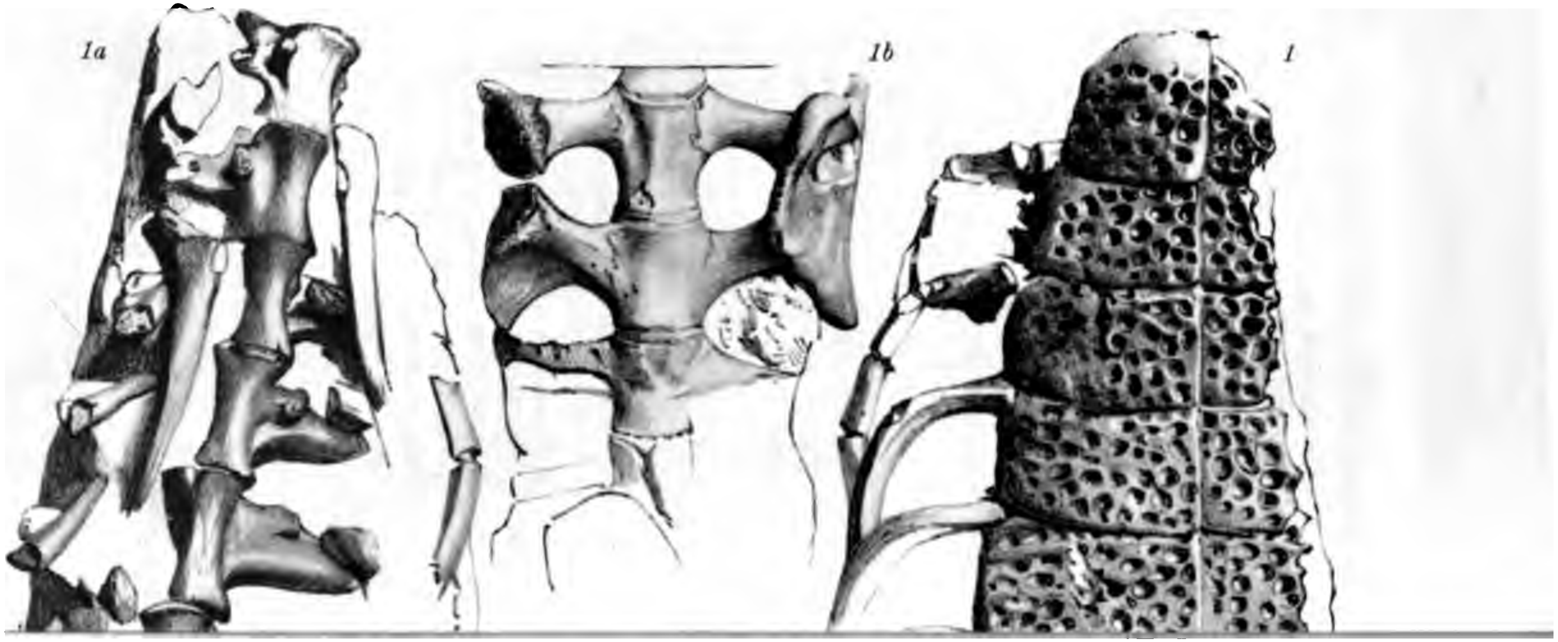

1a
1b
1

Fig. 4. *Stagonolepis.*—Cast of the impression of a radius or fibula. (Elgin Museum, No. 26.)
Fig. 5. *Stagonolepis.*—Cast of the impression of a metatarsal or metacarpal bone. (Elgin Museum, No. 48.)
Figs. 6, 6*a*. *Stagonolepis.*—Cast of the impression of a metatarsal (?) bone. (Elgin Museum, No. 23.)
Figs. 7, 7*a*. Cast of an impression of an anterior caudal vertebra. (Elgin Museum, No. 18.)

PLATE IX. [PLATE 16.]

Fig. 1. *Stagonolepis.*—The sandstone core; and Fig. 1*a*, the cavity which receives the opposite face of the core to that shown in the figure, of the specimen containing the fragment of the skull described at p. 17. (Museum of Practical Geology.)
Figs. 2, 2*a*. *Stagonolepis.*—Diagrammatic restorations of the palatal and lateral aspects of this fragment of the skull.
Fig. 3. *Stagonolepis.*—A portion of a maxilla with teeth. (Museum of Practical Geology.)
Figs. 4, 4*a*. *Stagonolepis.*—One of the maxillary teeth separately, of the natural size and magnified four times.
Fig. 5. Palatal view of the skull of *Gavialis Gangeticus.* (After D'Alton and Burmeister, *l.c.*)
Fig. 6. Palatal view of the skull of *Belodon.* (After Von Meyer, *l.c.*)
Fig. 7. Palatal view of the skull of *Sphenodon.* (After Günther. Philosophical Transactions of the Royal Society, vol. 157, pl. XXVI., fig. 2.)
In Figures 5, 6 and 7; *vo.*, vomer; *pl.*, palatine; *pt.*, pterygoid; *pn.*, primitive, and *s.p.n.*, secondary posterior nares.

PLATE X. [PLATE 17.]

(All the figures in this plate are taken from casts of impressions of bones of *Stagonolepis* from Lossiemouth, and are in the Museum of Practical Geology. Figs. 2 and 9 are of the natural size, the rest are reduced to half of the size of nature.)
Figs. 1, 1*a*. Lateral and posterior views of the ankylosed scapula and coracoid.
Figs. 2, 2*a*. Front and side views of the interclavicle.
Figs. 3 and 4. Ilia.
Figs. 5 and 5*a*. Lateral and anterior views of an ischium.
Fig. 6. The proximal end of a humerus.
Fig. 7. An incomplete humerus.
Fig. 8. A tibia (?).
Fig. 9. A metatarsal or metacarpal bone.
Fig. 10. A restoration of the posterior lumbar, the sacral, and the anterior caudal vertebræ from the specimen described at pp. 14, 15.

PLATES XI. AND XII. [PLATES 18, 19.]

In these plates I have given, for comparison with *Stagonolepis*, figures of the dermal armour, of the skull, and of some other parts of the skeleton of one of the oldest known *Mesosuchia*, the *Crocodilus temporalis* of De Blainville, *Teleosaurus temporalis* of M. Eudes Deslongchamps. It has been identified with the *Pelagosaurus typus* of Bronn by M. Eugene E. Deslongchamps.[1]

[1] 'Notes Paléontologiques,' vol. i., 1869.

Teleosaurus temporalis appears to have been a small animal, the largest known specimens hardly exceeding three feet in length. The species is confined to the Upper Lias.

The specimens represented in the Plates, formed part of the Tesson Collection, and are now in the British Museum. They have already been figured and described by M. Eudes Deslongchamps in his remarkable monograph[1] on the Teleosauria of the Jurassic epoch, which is supplemented in the "Notes Paléontologiques" of his son.

In his preliminary observations, M. Eudes Deslongchamps declares that his wish is far less to define species zoologically than to determine the anatomical relations of the *Teleosauria* with their nearest living allies, and he has admirably carried out his intention. Favoured with abundant materials, in an excellent state of preservation, he has compared the skeletons of the ancient reptiles, bone by bone, with their living analogues, and has traced out their resemblances and differences with a minuteness of detail which is but rarely practicable in palæontological inquiries.

The chief subject of M. Eudes Deslongchamps' investigations is the species of which parts are here figured.

M. Deslongchamps states that he found "en place et en rapport" (*l.c.* p. 65) the dorsal and ventral scutes represented in Plates XI. and XII., and he has described the manner in which the scutes have been adjusted into their present position. The scutes which are absent are indicated by outlines, in the construction of which M. Deslongchamps followed the analogy of the ventral armour of *Teleosaurus cadomensis*, with which he was already acquainted.

M. Deslongchamps, writing in 1856 (*l.c.* p. 63), appears to have learned that the Caimans and Jacares have ventral scutes from an article by the late Dr. J. E. Gray, published in the Annals and Magazines of Natural History for November 1862, and he says that the fact is not mentioned in any earlier work known to him. He appears to have overlooked the monograph of D'Alton and Burmeister, "Der fossile Gavial von Boll" (1854), to which I have referred in my first Memoir on *Stagonolepis*, no less than that essay itself, and another "On the specific and generic characters of recent Crocodilia," published in the "Proceedings of the Linnean Society" for 1859. The characters of the dermal armour of recent and extinct *Crocodilia* are fully discussed in these memoirs, with which Dr. J. E. Gray was perfectly well acquainted. D'Alton and Burmeister describe the ventral armour of a recent Crocodile (apparently a *Jacare*) with great accuracy, but they imagined that all recent Crocodilia possess a similar armour.

PLATE XI. [PLATE 18.]

Figs. 1, 1*a*, 1*b*. *Teleosaurus temporalis*.—Dorsal, ventral, and lateral views of the skull.

Fig. 2. *Teleosaurus temporalis*.—The ventral armour, consisting of flat, articulated scutes, the surfaces of which present indistinctly radiating pits.

PLATE XII. [PLATE 19.]

Fig. 1. *Teleosaurus temporalis*.—The thoraco-lumbar and anterior sacral dorsal scutes, with ribs.

Fig. 1*a*. The opposite face of the same specimen, exhibiting the vertebræ and ribs.

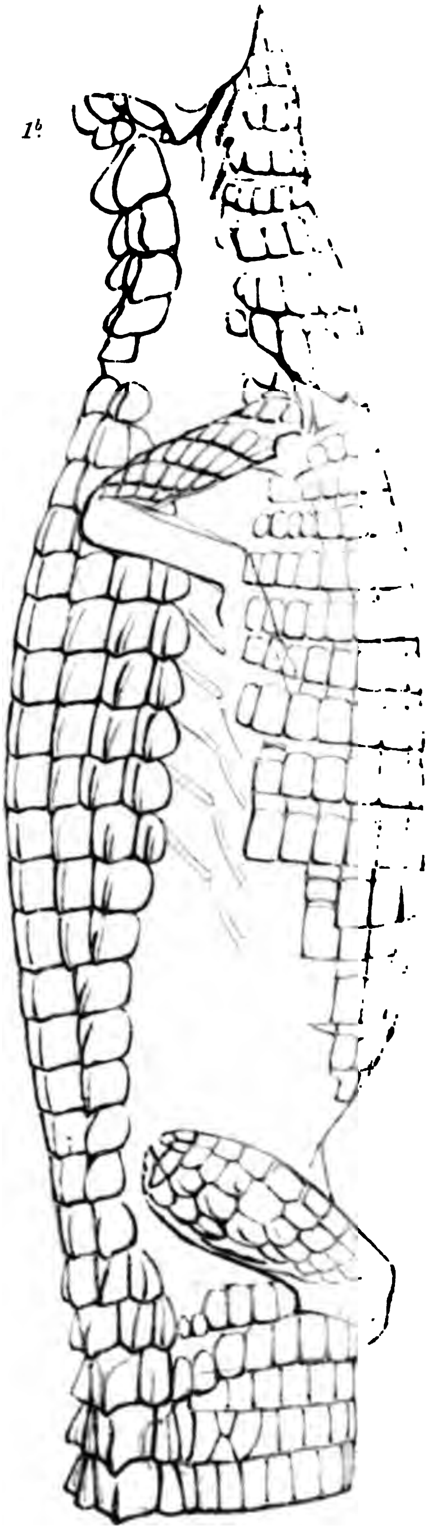
Fig. 1*b*. Ventral aspect of the sacral vertebræ, with one ilium in place, of the same specimen.

Fig. 1*c*. The posterior sacral and anterior caudal dorsal scutes of the same specimen.

Fig. 1*d*. Lateral view of the ilium.

[1] 'Mémoires sur les Téléosauriens de l'Époque Jurassique du Département du Calvados.' 'Mémoires de la Société Linnéenne de Normandie,' vol. xiii., 1864.

1b.



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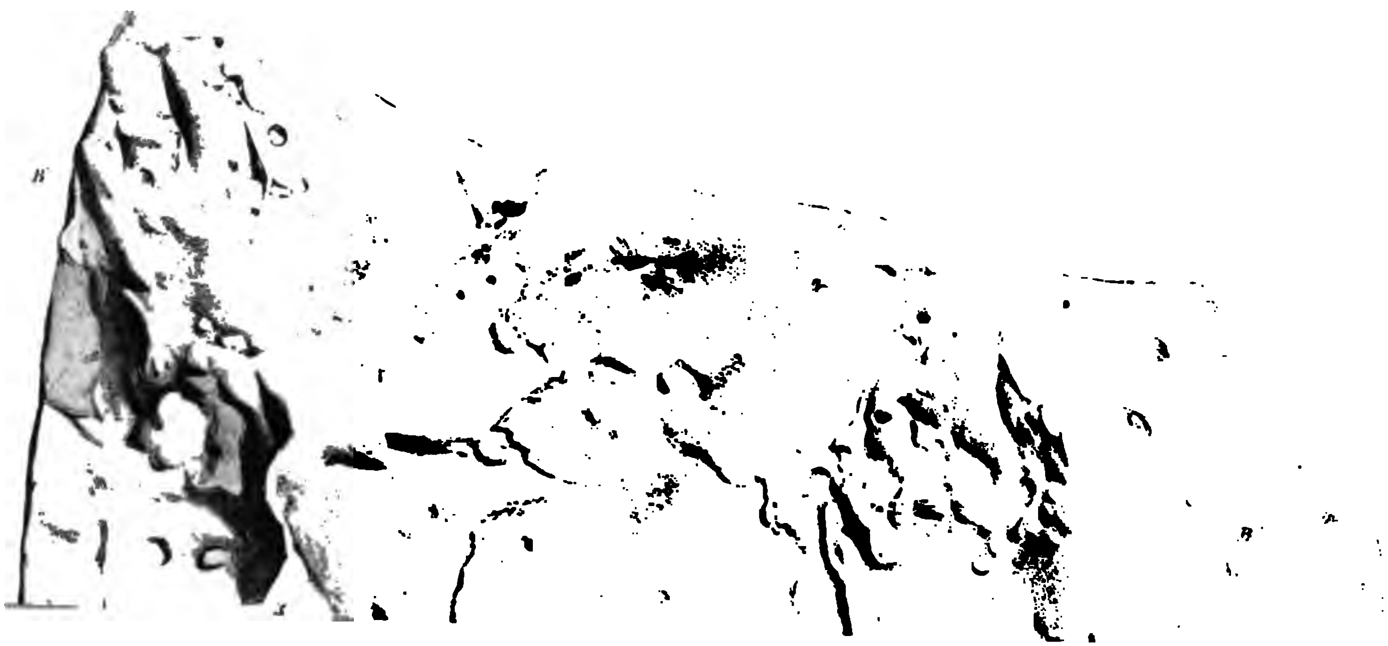
Geological Survey of the United Kingdom. [PLATE 21.] PLATE XIV



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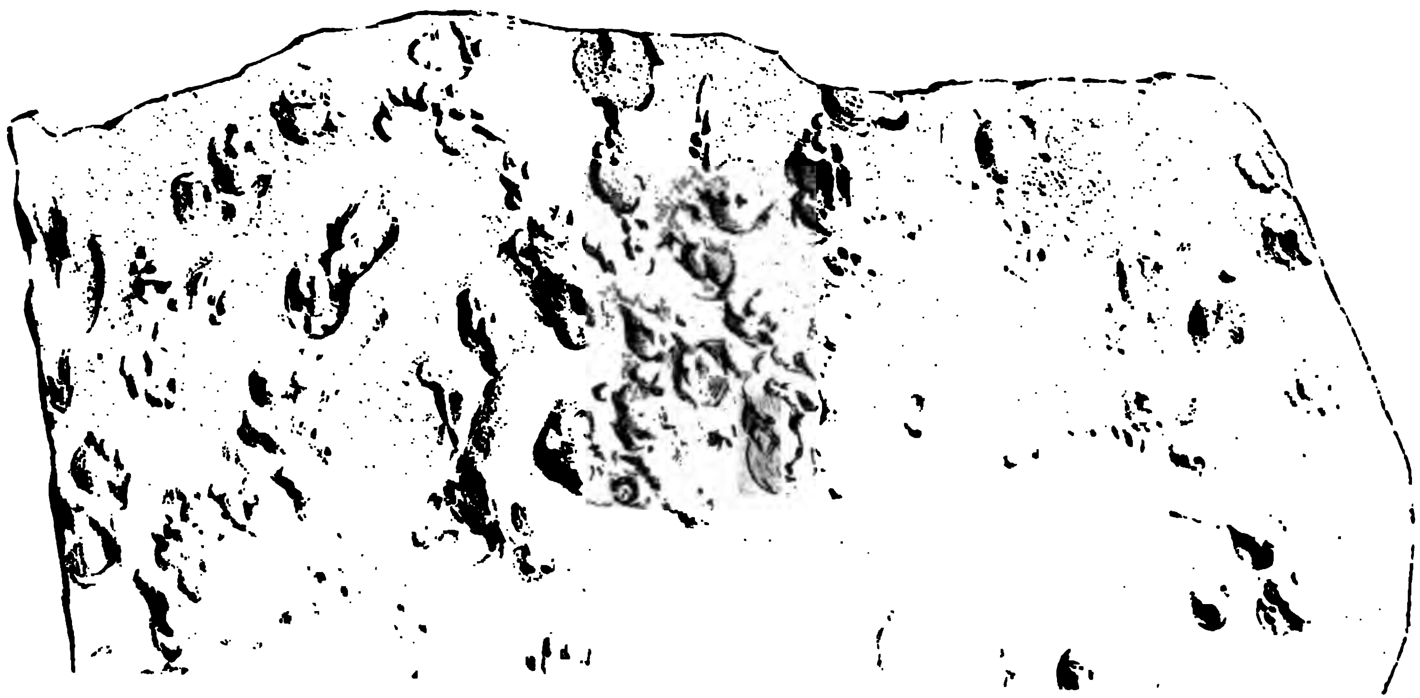

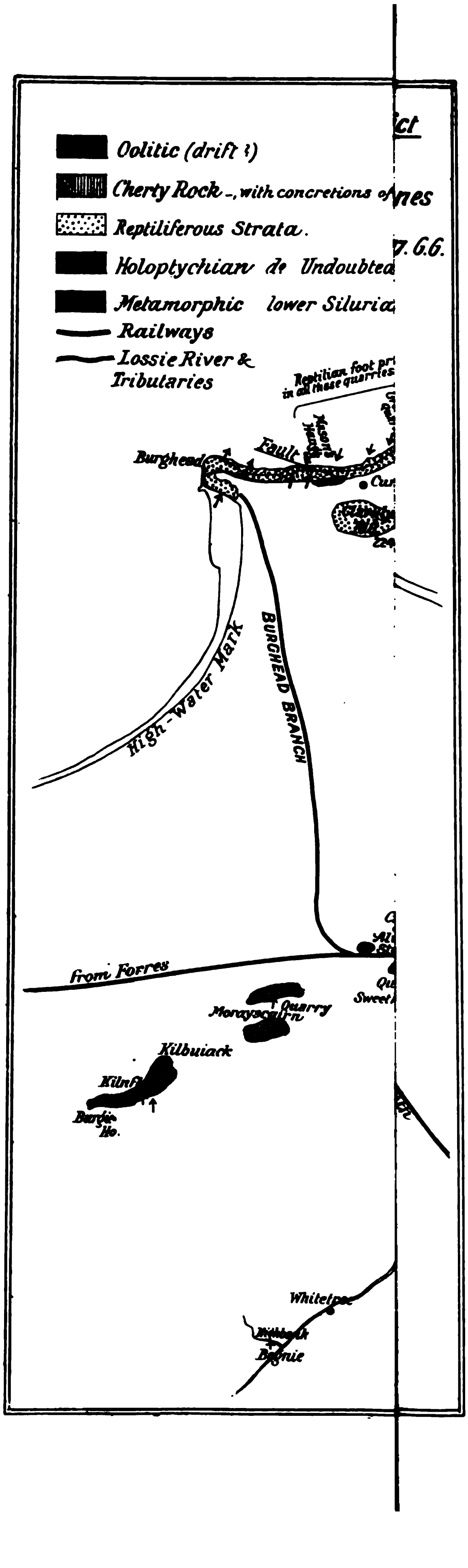

Oolitic (drift ?)
Cherty Rock -, with concretions of
Reptiliferous Strata.
Holoptychian do Undoubted
Metamorphic lower Silurian
Railways
Lossie River & Tributaries
Reptilian foot pri
in all these quarries
Fault
Burghead
High-Water Mark
BURGHEAD BRANCH
from Forres
Quarry
Moraysea
Kilbuiack
Kilnf
Burgie Ho.
Whitet
Bognie

PLATE XIII. [PLATE 20.]

Figs. 1, 1*a*, 1*b*. *Caiman palpebrosus.*—Dorsal, ventral, and lateral views of the dermal armour of the neck, trunk, and anterior part of the tail.

Figs. 1*c*, 1*d*. The dermal armour of the antebrachium and of the crus.

Fig. 1*e*. A dorsal scute enlarged, showing its ridge and sculpture.

Fig. 1*f*. A ventral scute enlarged, showing the articular facet, the suture between the anterior and the posterior portions, and the radiating grooves of the surface.

PLATE XIV. [PLATE 21.]

The footmarks from Cummingstone, described at p. 235.

PLATE XV. [PLATE 22.]

Figs. 1, 2, 3, 4. Footprints on the slab represented and similarly numbered in Plate XVI.; of the size of nature.

Fig. 5. Footmarks from Cummingstone from the same series as those represented in Plate XIV.

Fig. 6. A footmark from the same slab as the foregoing, made by a much larger animal.

PLATE XVI. [PLATE 23.]

The slab of sandstone from Cummingstone, exhibiting many tracks, described at pp. 50, 51. One fourth the size of nature.

[PLATE 24.]

Geological Sketch of the District of Elginshire in which Reptiliferous Sandstones appear.

XIV

ON THE STUDY OF BIOLOGY

Nature, vol. xv. 1877, *pp.* 219–224. (*Delivered at the South Kensington Museum, Saturday, December 16th,* 1876.)

IT is my duty to-night to speak about the study of Biology, and while it may be that there are many among you who are quite familiar with that study, yet as a lecturer of some standing, it would, I know by experience, be very bad policy on my part to suppose such to be extensively the case. On the contrary, I must imagine that there are many of you who would like to know what Biology is; that there will be others who have that amount of information, but would nevertheless gladly learn why it should be worth their while to study Biology; and yet others, again, to whom these two points are clear, but who desire to learn how they had best study it, and finally when they had best study it; and I shall address myself to the endeavour to give you some answer to these four questions—what Biology is, why it should be studied, how it should be studied, and when it should be studied.

In the first place, in respect to what Biology is, there are, I believe, some persons who imagine that the term "Biology" is simply a new-fangled denomination, a neologism in short for what used to be known under the title of "Natural History," but I shall try to show you, on the contrary, that the word is the expression of the growth of science during the last 200 years, and came into existence half a century ago.

At the revival of learning, knowledge was divided into two kinds—the knowledge of nature and the knowledge of man; for it was the current idea then (and a great deal of that ancient conception still remains) that there was a sort of essential antithesis, not to say antagonism, between nature and man; and that the two had not very

much to do with one another, except that the one was oftentimes exceedingly troublesome to the other. Though it is one of the salient merits of our great philosophers of the seventeenth century, that they recognise but one scientific method, applicable alike to man and to nature, we find this notion of the existence of a broad distinction between nature and man in the writings of Bacon and Hobbes of Malmesbury; and I have brought with me that famous work which is now so little known, greatly as it deserves to be studied, "The Leviathan," in order that I may put to you in the wonderfully terse and clear language of Thomas Hobbes, what was his view of the matter. He says:—

"The register of knowledge of fact is called history. Whereof there be two sorts, one called natural history; which is the history of such facts or effects of nature as have no dependence on man's will; such as are the histories of metals, plants, animals, regions, and the like. The other is civil history; which is the history of the voluntary actions of men in commonwealths."

So that all history of fact was divided into these two great groups of natural and of civil history. The Royal Society was in course of foundation about the time that Hobbes was writing this book, which was published in 1651, and that Society is termed a "Society for the Advancement of Natural Knowledge," which is nearly the same thing as a "Society for the Advancement of Natural History." As time went on, and the various branches of human knowledge became more distinctly developed and separated from one another, it was found that some were much more susceptible of precise mathematical treatment than others. The publication of the "Principia" of Newton, which probably gave a greater stimulus to physical science than any work ever published before, or which is likely to be published hereafter, showed that precise mathematical methods were applicable to those branches of science such as astronomy, and what we now call physics, which occupy a very large portion of the domain of what the older writers understood by natural history. And inasmuch as the partly deductive and partly experimental methods of treatment to which Newton and others subjected these branches of human knowledge, showed that the phenomena of nature which belonged to them were susceptible of explanation, and thereby came within the reach of what was called "philosophy" in those days; so much of this kind of knowledge as was not included under astronomy came to be spoken of as "natural philosophy"—a term which Bacon had employed in a much wider sense. Time went on, and yet other branches of science developed themselves. Chemistry took a definite

shape, and as all these sciences, such as astronomy, natural philosophy, and chemistry, were susceptible either of mathematical treatment or of experimental treatment, or of both, a great distinction was drawn between the experimental branches of what had previously been called natural history and the observational branches—those in which experiment was (or appeared to be) of doubtful use, and where, at that time, mathematical methods were inapplicable. Under these circumstances the old name of "Natural History" stuck by the residuum, by those phenomena which were not, at that time, susceptible of mathematical or experimental treatment; that is to say, those phenomena of nature which come now under the general heads of physical geography, geology, mineralogy, the history of plants, and the history of animals. It was in this sense that the term was understood by the great writers of the middle of the last century—Buffon and Linnæus—by Buffon in his great work, the "Histoire Naturelle Générale," and by Linnæus in his splendid achievement, the "Systema Naturæ." The subjects they deal with are spoken of as "Natural History," and they called themselves and were called "Naturalists." But you will observe that this was not the original meaning of these terms; but that they had, by this time, acquired a signification widely different from that which they possessed primitively.

The sense in which "Natural History" was used at the time I am now speaking of has, to a certain extent, endured to the present day. There are now in existence, in some of our northern universities, chairs of "Civil and Natural History," in which "Natural History" is used to indicate exactly what Hobbes and Bacon meant by that term. There are others in which the unhappy incumbent of the chair of Natural History is, or was, still supposed to cover the whole ground of geology and mineralogy, zoology, perhaps even botany in his lectures. But as science made the marvellous progress which it did make at the latter end of the last and the beginning of the present century, thinking men began to discern that under this title of "Natural History" there were included very heterogeneous constituents—that, for example, geology and mineralogy were, in many respects, widely different from botany and zoology; that a man might obtain an extensive knowledge of the structure and functions of plants and animals without having need to enter upon the study of geology and mineralogy, and *vice versâ*; and, further, as knowledge advanced, it became clear that there was a great analogy, a very close alliance, between those two sciences of botany and zoology which deal with living beings, while they are much more widely separated from all other studies. It is due to Buffon to remark that he clearly recognised this great fact.

He says: "ces deux genres d'êtres organisés [les animaux et les végétaux] ont beaucoup plus de propriétés communes que de différences réelles." Therefore, it is not wonderful that, at the beginning of the present century, and oddly enough in two different countries, and so far as I know, without any intercommunication, two famous men clearly conceived the notion of uniting the sciences which deal with living matter into one whole, and of dealing with them as one discipline. In fact I may say there were three men to whom this idea occurred contemporaneously, although there were but two who carried it into effect, and only one who worked it out completely. The persons to whom I refer were the eminent physiologist Bichat, the great naturalist Lamarck, in France; and a distinguished German, Treviranus. Bichat[1] assumed the existence of a special group of "physiological" sciences. Lamarck, in a work published in 1801,[2] for the first time made use of the name "Biologie" from the two Greek words which signify a discourse upon life and living things. About the same time, it occurred to Treviranus that all those sciences which deal with living matter are essentially and fundamentally one, and ought to be treated as a whole, and, in the year 1802, he published the first volume of what he also called "Biologie." Treviranus's great merit consists in this, that he worked out his idea, and wrote the very remarkable book to which I refer. It consists of six volumes, and occupied its author for twenty years—from 1802 to 1822.

That is the origin of the term "Biology," and that is how it has come about that all clear thinkers and lovers of consistent nomenclature have substituted for the old confusing name of "Natural History," which has conveyed so many meanings, the term "Biology," which denotes the whole of the sciences which deal with living things, whether they be animals or whether they be plants. Some little time ago—in the course of this year, I think—I was favoured by a learned classic, Dr. Field of Norwich, with a disquisition, in which he endeavoured to prove that, from a philological point of view, neither Treviranus nor Lamarck had any right to coin this new word "Biology" for their purpose; that, in fact, the Greek word "Bios" had relation only to human life and human affairs, and that a different word was employed when they wished to speak of the life of animals and plants. So Dr. Field tells us we are all wrong in using the term biology, and that we ought to employ another, only unluckily he is not quite sure about the propriety of that which he proposes as a sub-

[1] See the distinction between the "sciences physiques" and the "sciences physiologiques" in the 'Anatomie Générale,' 1801.

[2] 'Hydrogeologie,' an. x. (1801).

stitute. It is a somewhat hard one—zootocology. I am sorry we are wrong, because we are likely to continue so. In these matters we must have some sort of "Statute of Limitations." When a name has been employed for half-a-century, persons of authority[1] have been using it, and its sense has become well understood, I am afraid that people will go on using it, whatever the weight of philological objection.

Now that we have arrived at the origin of this word "Biology," the next point to consider is: What ground does it cover? I have said that in its strict technical sense it covers all the phenomena that are exhibited by living things, as distinguished from those which are not living; but while that is all very well so long as we confine ourselves to the lower animals and to plants, it lands us in a very considerable difficulty when we reach the higher forms of living things. For whatever view we may entertain about the nature of man, one thing is perfectly certain, that he is a living creature. Hence, if our definition is to be interpreted strictly, we must include man and all his ways and works under the head of Biology; in which case we should find that psychology, politics, and political economy, would be absorbed into the province of Biology. In fact, civil history would be merged in natural history. In strict logic it may be hard to object to this course, because no one can doubt that the rudiments and outlines of our own mental phenomena are traceable among the lower animals. They have their economy and their polity, and if, as is always admitted, the polity of bees and the commonwealth of wolves fall within the purview of the biologist proper, it becomes hard to say why we should not include therein human affairs, which in so many cases resemble those of the bees in zealous getting, and are not without a certain parity in the proceedings of the wolves. The real fact is that we biologists are a self-sacrificing people; and inasmuch as, on a moderate estimate, there are about a quarter of a million different species of animals and plants to know about already, we feel that we have more than sufficient territory. There has been a sort of practical convention by which we give up to a different branch of science what Bacon and Hobbes would have called "Civil History." That branch of science has constituted itself under the head of Sociology. I may use phraseology which at present will be well understood, and say that we have allowed that province of Biology to become autonomous; but I should like you to recollect that that is a sacrifice, and that you should

[1] "The term *Biology*, which means exactly what we wish to express, *the Science of Life*, has often been used and has of late become not uncommon among good writers."—Whewell, 'Philosophy of the Inductive Sciences,' vol. i. p. 544 (edition of 1847).

not be surprised if it occasionally happens that you see a biologist trespassing upon questions of philosophy or politics ; or meddling with human education ; because, after all, that is a part of his kingdom which he has only voluntarily forsaken.

Having now defined the meaning of the word Biology, and having indicated the general scope of Biological Science, I turn to my second question, which is—Why should we study Biology? Possibly the time may come when that will seem a very odd question. That we, living creatures, should not feel a certain amount of interest in what it is that constitutes our life will eventually, under altered ideas of the fittest objects of human inquiry, seem to be a singular phenomenon ; but at present, judging by the practice of teachers and educators, this would seem to be a matter that does not concern us at all. I propose to put before you a few considerations which I dare say many of you will be familiar with already, but which will suffice to show—not fully, because to demonstrate this point fully would take a great many lectures—that there are some very good and substantial reasons why it may be advisable that we should know something about this branch of human learning. I myself entirely agree with another sentiment of the philosopher of Malmesbury, "that the scope of all speculation is the performance of some action or thing to be done," and I have not any very great respect for, or interest in, mere knowing as such. I judge of the value of human pursuits by their bearing upon human interests ; in other words, by their utility, but I should like that we should quite clearly understand what it is that we mean by this word "utility." Now in an Englishman's mouth it generally means that by which we get pudding or praise, or both. I have no doubt that is one meaning of the word utility, but it by no means includes all I mean by utility. I think that knowledge of every kind is useful in proportion as it tends to give people right ideas, which are essential to the foundation of right practice, and to remove wrong ideas, which are the no less essential foundations and fertile mothers of every description of error in practice. And inasmuch as, whatever practical people may say, this world is, after all, absolutely governed by ideas, and very often by the wildest and most hypothetical ideas, it is a matter of the very greatest importance that our theories of things, and even of things that seem a long way apart from our daily lives, should be as far as possible true, and as far as possible removed from error. It is not only in the coarser practical sense of the word "utility," but in this higher and broader sense that I measure the value of the study of biology by its utility, and I shall try to point out to you that you will feel the need of some knowledge of Biology at a great many turns

of this present nineteenth century life of ours. For example, most of us lay great and very just stress upon the conception which is entertained of the position of man in this universe and his relation to the rest of nature. We have almost all of us been told, and most of us hold by the tradition, that man occupies an isolated and peculiar position in nature; that though he is in the world he is not of the world; that his relations to things about him are of a remote character, that his origin is recent, his duration likely to be short, and that he is the great central figure round which other things in this world revolve. But this is not what the biologist tells us. At the present moment you will be kind enough to separate me from them, because it is in no way essential to my argument just now that I should advocate their views. Don't suppose that I am saying this for the purpose of escaping the responsibility of their beliefs, because at other times and in other places I do not think that point has been left doubtful; but I want clearly to point out to you that for my present argument they may all be wrong; nevertheless, my argument will hold good. The biologists tell us that all this is an entire mistake. They turn to the physical organisation of man. They examine his whole structure, his bony frame, and all that clothes it. They resolve him into the finest particles into which the microscope will enable them to break him up. They consider the performance of his various functions and activities, and they look at the manner in which he occurs on the surface of the world. Then they turn to other animals and taking the first handy domestic animal—say a dog—they profess to be able to demonstrate that the analysis of the dog leads them, in gross, to precisely the same results as the analysis of the man; that they find almost identically the same bones, having the same relations; that they can name the muscles of the dog by the names of the muscles of the man, and the nerves of the dog by those of the nerves of the man, and that such structures and organs of sense as we find in the man such also we find in the dog; they analyse the brain and spinal cord, and they find that the nomenclature which fits the one answers for the other. They carry their microscopic inquiries in the case of the dog as far as they can, and they find that his body is resolvable into the same elements as those of the man. Moreover, they trace back the dog's and the man's development, and they find that, at a certain stage of their existence, the two creatures are not distinguishable the one from the other; they find that the dog and his kind have a certain distribution over the surface of the world comparable in its way to the distribution of the human species. What is true of the dog they tell us is true of all the higher

animals; and they assert that for the whole of these creatures they can lay down a common plan, and regard the man and the dog, and the horse and the ox as minor modifications of one great fundamental unity. Moreover, the investigations of the last three-quarters of a century have proved, they tell us, that similar inquiries carried out through all the different kinds of animals which are met with in nature will lead us, not in one straight series, but by many roads, step by step, gradation by gradation, from man, at the summit, to specks of animated jelly at the bottom of the series; so that the idea of Leibnitz and of Bonnet, that animals form a great scale of being, in which there are a series of gradations from the most complicated form to the lowest and simplest; that idea, though not exactly in the form in which it was propounded by those philosophers, turns out to be substantially correct. More than this, when biologists pursue their investigations into the vegetable world, they find that they can, in the same way, follow out the structure of the plant from the most gigantic and complicated trees down, through a similar series of gradations, until they arrive at specks of animated jelly, which they are puzzled to distinguish from those specks which they reached by the animal road.

Thus, biologists have arrived at the conclusion that a fundamental uniformity of structure pervades the animal and vegetable worlds, and that plants and animals differ from one another simply as modifications of the same great general plan.

Again, they tell us the same story in regard to the study of function. They admit the large and important interval which, at the present time, separates the manifestations of the mental faculties observable in the higher forms of mankind, and even in the lower forms, such as we know them, mentally from those exhibited by other animals; but, at the same time, they tell us that the foundations or rudiments of almost all the faculties of man are to be met with in the lower animals; that there is a unity of mental faculty as well as of bodily structure, and that, here also, the difference is a difference of degree and not of kind. I said "almost all" for a reason. Among the many distinctions which have been drawn between the lower creatures and ourselves, there is one which is hardly ever insisted on,[1] but which may be very fitly spoken of in a place so largely devoted to art as that in which we are assembled. It is this, that while among various kinds of animals it is possible to discover traces of all the other faculties of man, especially the faculty of mimicry, yet that particular form of mimicry, which shows itself in the imitation of form either

[1] I think that Prof. Allman was the first to draw attention to it.

by modelling or by drawing is not to be met with. As far as I know, there is no sculpture or modelling, and decidedly no painting or drawing, of animal origin. I mention the fact, in order that such comfort may be derived therefrom as artists may feel inclined to take.

If what the biologists tell us is true, it will be needful for us to get rid of our erroneous conceptions of man and of his place in nature, and substitute right ones for them. But it is impossible to form any judgment as to whether the biologists are right or wrong unless we are able to appreciate the nature of the arguments which they have to offer.

One would almost think that this was a self-evident proposition. I wonder what a scholar would say to the man who should undertake to criticise a difficult passage in a Greek play but who obviously had not acquainted himself with the rudiments of Greek grammar. And yet before giving positive opinions about these high questions of Biology people not only don't seem to think it necessary to be acquainted with the grammar of the subject, but they have not even mastered the alphabet. You find criticism and denunciation showered about by persons who not only have not attempted to go through the discipline necessary to enable them to be judges, but have not even reached that stage of emergence from ignorance in which the knowledge that such a discipline is necessary dawns upon the mind. I have had to watch with some attention—in fact I have been favoured with a good deal of it myself—the sort of criticism with which biologists and biological teachings are visited. I am told every now and then that there is a "brilliant article"[1] in so-and-so, in which we are all demolished. I used to read these things once, but I am getting old now, and I have ceased to attend very much to this cry of "wolf." When one does read any of these productions, what one finds generally, on the face of it, is that the brilliant critic is devoid of even the elements of biological knowledge, and that his brilliancy is like the light given out by the crackling of thorns under a pot of which Solomon speaks. So far as I recollect Solomon makes use of that image for purposes of comparison; but I won't proceed further into that matter.

Two things must be obvious: in the first place, that every man who has the interests of truth at heart must earnestly desire that every well-founded and just criticism that can be made should be made;

[1] Galileo was troubled by a sort of people whom he called "paper philosophers," because they fancied that the true reading of nature was to be detected by the collation of texts. The race is not extinct, but, as of old, brings forth its "winds of doctrine" by which the weathercock heads among us are much exercised.

but that, in the second place, it is essential to anybody's being able to benefit by criticism that the critic should know what he is talking about and be in a position to form a mental image of the facts symbolised by the words he uses. If not, it is as obvious in the case of a biological argument as it is in that of a historical or philological discussion, that such criticism is a mere waste of time on the part of its author, and wholly undeserving of attention on the part of those who are criticised. Take it then as an illustration of the importance of biological study, that thereby alone are men able to form something like a rational conception of what constitutes valuable criticism of the teachings of biologists.[1]

Next, I may mention another bearing of biological knowledge—a more practical one in the ordinary sense of the word. Consider the theory of infectious disease. Surely that is of interest to all of us. Now the theory of infectious diseases is rapidly being elucidated by biological study. It is possible to produce from among the lower animals cases of devastating disease, which have all the appearance of our infectious diseases, and which are certainly and unmistakably caused by living organisms. This fact renders it possible, at any rate, that that doctrine of the causation of infectious disease which is known under the name of "the germ theory" may be well-founded; and if so it must needs lead to the most important practical measures in dealing with those most terrible visitations. It may be well that the general as well as the professional public should have a sufficient knowledge of biological truths to be able to take a rational interest in the discussion of such problems, and to see, what I think they may hope to see, that to those who possess a sufficient elementary knowledge of Biology, they are not all quite open questions.

Let me mention another important practical illustration of the

[1] Some critics do not even take the trouble to read. I have recently been adjured with much solemnity, to state publicly why I have "changed" my opinion as to the value of the palæontological evidence of the occurrence of evolution.

To this my reply is. Why should I when that statement was made seven years ago? An address delivered from the Presidential Chair of the Geological Society in 1870 may be said to be a public document, inasmuch as it not only appeared in the *Journal* of that learned body, but was re-published in 1873 in a volume of 'Critiques and Addresses,' to which my name is attached. Therein will be found a pretty full statement of my reasons for enunciating two propositions: (1) that "when we turn to the higher *Vertebrata*, the results of recent investigations, however we may sift and criticise them, seem to me to leave a clear balance in favour of the evolution of living forms one from another;" and (2) that the case of the horse is one which "will stand rigorous criticism."

Thus I do not see clearly in what way I can be said to have changed my opinion, except in the way of intensifying it, when in consequence of the accumulation of similar evidence since 1870, I recently spoke of the denial of evolution as not worth serious consideration.

value of biological study. Within the last forty years the theory of agriculture has been revolutionised. The researches of Liebig, and those of our own Lawes and Gilbert, have had a bearing upon that branch of industry the importance of which cannot be over-estimated; but the whole of these new views have grown out of the better explanation of certain processes which go on in plants, and which of course form a part of the subject-matter of Biology.

I might go on multiplying these examples, but I see that the clock won't wait for me, and I must therefore pass to the third question to which I referred :—Granted that Biology is something worth studying, what is the best way of studying it? Here I must point out that, since Biology is a physical science, the method of studying it must needs be analogous to that which is followed in the other physical sciences. It has now long been recognised that if a man wishes to be a chemist it is not only necessary that he should read chemical books and attend chemical lectures, but that he should actually for himself perform the fundamental experiments in the laboratory, and know exactly what the words which he finds in his books and hears from his teachers, mean. If he does not do that he may read till the crack of doom, but he will never know much about chemistry. That is what every chemist will tell you, and the physicist will do the same for his branch of science. The great changes and improvements in physical and chemical scientific education which have taken place of late have all resulted from the combination of practical teaching with the reading of books and with the hearing of lectures. The same thing is true in Biology. Nobody will ever know anything about Biology except in a dilettante "paper philosopher" way, who contents himself with reading books on botany, zoology, and the like; and the reason of this is simple and easy to understand. It is that all language is merely symbolical of the things of which it treats; the more complicated the things, the more bare is the symbol, and the more its verbal definition requires to be supplemented by the information derived directly from the handling, and the seeing, and the touching of the thing symbolised: —that is really what is at the bottom of the whole matter. It is plain common sense, as all truth, in the long run is only common sense clarified. If you want a man to be a tea merchant, you don't tell him to read books about China or about tea, but you put him into a tea-merchant's office where he has the handling, the smelling, and the tasting of tea. Without the sort of knowledge which can be gained only in this practical way his exploits as a tea merchant will soon come to a bankrupt termination. The "paper philosophers" are under the delusion that physical science can be mastered as literary

accomplishments are acquired, but unfortunately it is not so. You may read any quantity of books, and you may be almost as ignorant as you were at starting, if you don't have, at the back of your minds, the change for words in definite images which can only be acquired through the operation of your observing faculties on the phenomena of nature.

It may be said :—" That is all very well, but you told us just now that there are probably something like a quarter of a million different kinds of living and extinct animals and plants, and a human life could not suffice for the examination of one-fiftieth part of all these." That is true, but then comes the great convenience of the way things are arranged ; which is, that although there are these immense numbers of different kinds of living things in existence, yet they are built up, after all, upon marvellously few plans.

There are, I suppose, about 100,000 species of insects, if not more, and yet anybody who knows one insect—if a properly chosen one—will be able to have a very fair conception of the structure of the whole. I do not mean to say he will know that structure thoroughly or as well as it is desirable he should know it, but he will have enough real knowledge to enable him to understand what he reads, to have genuine images in his mind of those structures which become so variously modified in all the forms of insects he has not seen. In fact, there are such things as types of form among animals and vegetables, and for the purpose of getting a definite knowledge of what constitutes the leading modifications of animal and plant life it is not needful to examine more than a comparatively small number of animals and plants.

Let me tell you what we do in the biological laboratory in the building adjacent to this. There I lecture to a class of students daily for about four-and-a-half months, and my class have, of course, their text-books ; but the essential part of the whole teaching, and that which I regard as really the most important part of it, is a laboratory for practical work, which is simply a room with all the materials arranged for ordinary dissection. We have tables properly arranged in regard to light, microscopes, and dissecting instruments, and we work through the structure of a certain number of animals and plants. As, for example, among the plants, we take a yeast plant, a *Protococcus*, a common mould, a *Chara*, a fern, and some flowering plant ; among animals we examine such things as an amæba, a *vorticella*, and a fresh-water polype. We dissect a star-fish, an earth-worm, a snail, a squid and a fresh-water mussel. We examine a lobster and a cray-fish, and a black beetle. We go on to a common skate, a cod-fish, a frog, a tortoise, a pigeon, and a rabbit, and that takes us about all the

time we have to give. The purpose of this course is not to make skilled dissectors, but to give every student a clear and definite conception, by means of sense-images, of the characteristic structure of each of the leading modifications of the animal kingdom; and that is perfectly possible, by going no further than the length of that list of forms which I have enumerated. If a man knows the structure of the animals I have mentioned, he has a clear and exact, however, limited, apprehension of the essential features of the organisation of all those great divisions of the animal and vegetable kingdoms to which the forms I have mentioned severally belong. And it then becomes possible for him to read with profit, because every time he meets with the name of a structure, he has a definite image in his mind of what the name means in the particular creature he is reading about, and therefore the reading is not mere reading. It is not mere repetition of words; but every term employed in the description, we will say, of a horse or of an elephant, will call up the image of the things he had seen in the rabbit, and he is able to form a distinct conception of that which he has not seen as a modification of that which he has seen.

I find this system to yield excellent results; and I have no hesitation whatever in saying, that any one who has gone through such a course, attentively, is in a better position to form a conception of the great truths of Biology, especially of morphology (which is what we chiefly deal with), than if he had merely read all the books on that topic put together.

The connection of this discourse with the Loan Collection of Scientific Apparatus arises out of the exhibition in that collection of certain aids to our laboratory work. Such of you as have visited that very interesting collection may have noticed a series of diagrams and of preparations illustrating the structure of a frog. Those diagrams and preparations have been made for the use of the students in the biological laboratory. Similar diagrams and preparations illustrating the structure of all the other forms of life we examine, are either made or in course of preparation. Thus the student has before him, first, a picture of the structure he ought to see, secondly, the structure itself worked out; and if with these aids, and such needful explanations and practical hints as a demonstrator can supply, he cannot make out the facts for himself in the materials supplied to him, he had better take to some other pursuit than that of biological science.

I should have been glad to have said a few words about the use of museums in the study of Biology, but I see that my time is

becoming short, and I have yet another question to answer. Nevertheless I must, at the risk of wearying you, say a word or two upon the important subject of museums. Without doubt there are no helps to the study of Biology, or rather to some branches of it, which are, or may be, more important than natural history museums; but, in order to take this place in regard to Biology, they must be museums of the future. The museums of the present do not do by any means so much for us as they might do. I do not wish to particularise, but I dare say many of you seeking knowledge, or in the laudable desire to employ a holiday usefully, have visited some great natural history museum. You have walked through a quarter of a mile of animals more or less well stuffed, with their long names written out underneath them, and, unless your experience is very different from that of most people, the upshot of it all is that you leave that splendid pile with sore feet, a bad headache, and a general idea that the animal kingdom is a " mighty maze without a plan." I do not think that a museum which brings about this result does all that may be reasonably expected of such an institution. What is needed in a collection of natural history is that it should be made as accessible and as useful as possible, on the one hand to the general public, and on the other to scientific workers. That need is not met by constructing a sort of happy hunting-ground of miles of glass cases, and, under the pretence of exhibiting everything, putting the maximum amount of obstacle in the way of those who wish properly to see anything.

What the public want is easy and unhindered access to such a collection as they can understand and appreciate; and what the men of science want is similar access to the materials of science. To this end the vast mass of objects of natural history should be divided into two parts—one open to the public, the other to men of science, every day. The former division should exemplify all the more important and interesting forms of life. Explanatory tablets should be attached to them, and catalogues containing clearly-written popular expositions of the general significance of the objects exhibited should be provided. The latter should contain, packed into a comparatively small space, in rooms adapted for working purposes, the objects of purely scientific interest. For example, we will say I am an ornithologist. I go to examine a collection of birds. It is a positive nuisance to have them stuffed. It is not only sheer waste, but I have to reckon with the ideas of the bird-stuffer, while, if I have the skin and nobody has interfered with it I can form my own judgment as to what the bird was like. For ornithological purposes what is needed is not glass cases full of stuffed birds on perches, but convenient

drawers into each of which a great quantity of skins will go. They occupy no great space and do not require any expenditure beyond their original cost. But for the purpose of the public, who want to learn indeed, but do not seek for minute and technical knowledge, the case is different. What one of the general public walking into a collection of birds desires to see is not all the birds that can be got together. He does not want to compare a hundred species of the sparrow tribe side by side; but he wishes to know what a bird is, and what are the great modifications of bird structure, and to be able to get at that knowledge easily. What will best serve his purpose is a comparatively small number of birds carefully selected, and artistically, as well as accurately, set up; with their different ages, their nests, their young, their eggs, and their skeletons side by side; and in accordance with the admirable plan which is pursued in this museum, a tablet, telling the spectator in legible characters what they are and what they mean. For the instruction and recreation of the public such a typical collection would be of far greater value than any many-acred imitation of Noah's ark.

Lastly comes the question as to when biological study may best be pursued. I do not see any valid reason why it should not be made, to a certain extent, a part of ordinary school training. I have long advocated this view, and I am perfectly certain that it can be carried out with ease, and not only with ease, but with very considerable profit to those who are taught; but then such instruction must be adapted to the minds and needs of the scholars. They used to have a very odd way of teaching the classical languages when I was a boy. The first task set you was to learn the rules of the Latin grammar in the Latin language—that being the language you were going to learn! I thought then that this was an odd way of learning a language, but did not venture to rebel against the judgment of my superiors. Now, perhaps, I am not so modest as I was then, and I allow myself to think that it was a very absurd fashion. But it would be no less absurd if we were to set about teaching Biology by putting into the hands of boys a series of definitions of the classes and orders of the animal kingdom, and making them repeat them by heart. That is a very favourite method of teaching, so that I sometimes fancy the spirit of the old classical system has entered into the new scientific system, in which case I would much rather that any pretence at scientific teaching were abolished altogether. What really has to be done is to get into the young mind some notion of what animal and vegetable life is. You have to consider in this matter practical convenience as well as other things. There are difficulties in the way of a lot of boys making messes

with slugs and snails ; it might not work in practice. But there is a very convenient and handy animal which everybody has at hand, and that is himself; and it is a very easy and simple matter to obtain common plants. Hence the broader facts of anatomy and physiology can be taught to young people in a very real fashion by dealing with the broad facts of human structure. Such viscera as they cannot very well examine in themselves, such as hearts, lungs, and livers, may be obtained from the nearest butcher's shop. In respect to teaching something about the biology of plants, there is no practical difficulty, because almost any of the common plants will do, and plants do not make a mess—at least they do not make an unpleasant mess ; so that, in my judgment, the best form of Biology for teaching to very young people is elementary human physiology on the one hand, and the elements of botany on the other ; beyond that I do not think it will be feasible to advance for some time to come. But then I see no reason why in secondary schools, and in the Science Classes which are under the control of the Science and Art Department—and which I may say, in passing, have, in my judgment, done so very much for the diffusion of a knowledge over the country—I think that in those cases we may go further, and we may hope to see instruction in the elements of Biology carried out, not perhaps to the same extent, but still upon somewhat the same principle as we do here. There is no difficulty, when you have to deal with students of the ages of 15 or 16, in practising a little dissection and getting a notion, at any rate, of the four or five great modifications of the animal form, and the like is true in regard to plants.

While, lastly, to all those who are studying biological science with a view to their own edification merely, or with the intention of becoming zoologists or botanists ; to all those who intend to pursue physiology —and especially to those who propose to employ the working years of their lives in the practice of medicine—I say that there is no training so fitted, or which may be of such important service to them, as the thorough discipline in practical biological work which I have sketched out as being pursued in the laboratory hard by.

I may add that, beyond all these different classes of persons who may profit by the study of Biology, there is yet one other. I remember, a number of years ago, that a gentleman who was a vehement opponent of Mr. Darwin's views and had written some terrible articles against them, applied to me to know what was the best way in which he could acquaint himself with the strongest arguments in favour of evolution. I wrote back, in all good faith and simplicity, recommending him to go through a course of comparative

anatomy and physiology, and then to study development. I am sorry to say he was very much displeased, as people often are with good advice. Notwithstanding this discouraging result, I venture, as a parting word, to repeat the suggestion, and to say to all the more or less acute lay and clerical "paper philosophers"[1] who venture into the regions of biological controversy—Get a little sound, thorough, practical, elementary instruction in Biology.

[1] Writers of this stamp are fond of talking about the Baconian method. I beg them therefore to lay to heart these two weighty sayings of the herald of Modern Science:—

"Syllogismus ex propositionibus constat, propositiones ex verbis, verba notionum tesseræ sunt. Itaque si notiones ipsæ (*id quod basis rei est*) confusæ sint et temere a rubus abstractæ, nihil in iis quæ superstruuntur est firmitudinis."—'Novum Organon,' ii. 14.

"Huic autem vanitati nonnulli ex modernis summa levitate ita indulserunt, ut in primo capitulo Geneseos et in libro Job et aliis scripturis sacris, philosophiam naturalem fundare conati sint; *inter vivos quærentes mortua.*"—*Ibid.* 65.

XV

ADDRESS TO THE ANTHROPOLOGICAL DEPARTMENT OF THE BRITISH ASSOCIATION, DUBLIN, 1878. INFORMAL REMARKS ON THE CONCLUSIONS OF ANTHROPOLOGY

Nature, vol. xviii., 1878, *pp.* 445–448.

WHEN I undertook, with the greatest possible pleasure, to act as a lieutenant of my friend the president of this Section, I steadfastly purposed to confine myself to the modest and useful duties of that position. For reasons with which it is not worth while to trouble you, I did not propose to follow the custom which has grown up in the Association of delivering an address upon the occasion of taking the chair of a section or department. In clear memory of the admirable addresses which you have had the privilege of hearing from Prof. Flower, and just now from Dr. M'Donnell, I cannot doubt that that practice is a very good one; but I would venture to say, to use a term of philosophy, that it looks very much better from an objective than from a subjective point of view. But I found that my resolution, like a great many good resolutions that I have made in the course of my life, came to very little, and that it was thought desirable that I should address you in some way. But I must beg of you to understand that this is no formal address. I have simply announced it as a few introductory remarks, and I must ask you to forgive whatever of crudity and imperfection there may be in the mode of expression of what I have to say, although naturally I shall do my best to take care that there is neither crudity nor inaccuracy in the substance of it. It has occurred to me that I might address myself to a point in connection with the business of this department which forces itself more or less upon the attention of everybody, and which, unless the bellicose instincts of human nature are less marked on this side of St. George's Channel than on the

other, may possibly have something to do with the large audiences we are always accustomed to see in the anthropological department. In the Geological Section I have no doubt it will be pointed out to you, or, at any rate, such knowledge may crop up incidentally, that there are on the earth's surface what are called *loci* of disturbance, where, for long ages, cataclysms and outbursts of lava and the like take place. Then everything subsides into quietude; but a similar disturbance is set up elsewhere. In Antrim, at the middle of the tertiary epoch, there was such a great centre of physical disturbance. We all know that at the present time the earth's crust, at any rate, is quiet in Antrim, while the great centres of local disturbance are in Sicily, in Southern Italy, in the Andes, and elsewhere. My experience of the British Association does not extend quite over a geological epoch, but it does go back rather longer than I care to think about; and when I first knew the British Association, the *locus* of disturbance in it was the Geological Section. All sorts of terrible things about the antiquity of the earth, and I know not what else, were being said there, which gave rise to terrible apprehensions. The whole world, it was thought, was coming to an end, just as I have no doubt that, if there were any human inhabitants of Antrim in the middle of the tertiary epoch, when those great lava streams burst out, they would not have had the smallest question that the whole universe was going to pieces. Well, the universe has not gone to pieces. Antrim is, geologically speaking, a very quiet place now, as well cultivated a place as one need see, and yielding abundance of excellent produce; and so, if we turn to the Geological Section, nothing can be milder than the proceedings of that admirable body. All the difficulties that they seemed to have encountered at first have died away, and statements that were the horrible paradoxes of that generation are now the commonplaces of schoolboys. At present the *locus* of disturbance is to be found in the Biological Section, and more particularly in the anthropological department of that Section. History repeats itself, and precisely the same terrible apprehensions which were expressed by the aborigines of the Geological Section, in long far back time, is at present expressed by those who attend our deliberations. The world is coming to an end, the basis of morality is being shaken, and I don't know what is not to happen if certain conclusions which appear probable are to be verified. Well, now, whoever may be here thirty years hence—I certainly cannot—but, depend upon it, whoever may be speaking at the meeting of this department of the British Association thirty years hence will find, exactly as the members of the Geological Section have found, on

looking back thirty years, that the very paradoxes and conclusions, and other horrible things that are now thought to be going to shake the foundations of the world will by that time have become parts of every-day knowledge and will be taught in our schools as accepted truth, and nobody will be one whit the worse.

The considerations which I think it desirable to put before you in order to show the foundations of the conclusions at which I have very confidently arrived, are of two kinds. The first is a reason based entirely upon philosophical considerations, namely, this—that the region of pure physical science, and the region of those questions which specially interest ordinary humanity, are apart, and that the conclusions reached in the one have no direct effect in the other. If you acquaint yourself with the history of philosophy, and with the endless variations of human opinion therein recorded, you will find that there is not a single one of those speculative difficulties which at the present time torment many minds as being the direct product of scientific thought, which is not as old as the times of Greek philosophy, and which did not then exist as strongly and as clearly as they do now, though they arose out of arguments based upon merely philosophical ideas. Whoever admits these two things—as everybody who looks about him must do—whoever takes into account the existence of evil in this world and the law of causation—has before him all the difficulties that can be raised by any form of scientific speculation. And these two difficulties have been occupying the minds of men ever since man began to think. The other consideration I have to put before you is that, whatever may be the results at which physical science as applied to man shall arrive, those results are inevitable—I mean that they arise out of the necessary progress of scientific thought as applied to man. You all, I hope, had the opportunity of hearing the excellent address which was given by our president yesterday, in which he traced out the marvellous progress of our knowledge of the higher animals which has been effected since the time of Linnæus. It is no exaggeration to say that at this present time the merest tyro knows a thousand times as much on the subject as is contained in the work of Linnæus, which was then the standard authority. Now how has that been brought about? If you consider what zoology, or the study of animals, signifies, you will see that it means an endeavour to ascertain all that can be studied, all the answers that can be given respecting any animal under four possible points of view. The first of these embraces considerations of structure. An animal has a certain structure, a certain mode of development, which means a series of stages in that structure. In the second place, every animal

exhibits a great number of active powers, the knowledge of which constitutes its physiology; and under those active powers we have, as physiologists, not only to include such matters as have been referred to by Dr. M'Donnell in his observations, but to take into account other kinds of activity. I see it announced that the Zoological Section of to-day is to have a highly interesting paper by Sir John Lubbock on the habits of ants. Ants have a polity, and exhibit a certain amount of intelligence, and all these matters are proper subjects for the study of the zoologist as far as he deals with the ant. There is yet a third point of view in which you may regard every animal. It has a distribution. Not only is it to be found somewhere on the earth's surface, but palæontology tells us, if we go back in time, that the great majority of animals have had a past history—that they occurred in epochs of the world's history far removed from the present. And when we have acquired all that knowledge which we may enumerate under the heads of anatomy, physiology, and distribution, there remains still the problem of problems to the zoologist, which is the study of the causes of those phenomena, in order that we may know how those things came about. All these different forms of knowledge and inquiry are legitimate subjects for science, there being no subject which is an illegitimate subject for scientific inquiry, except such as involves a contradiction in terms, or is itself absurd. Indeed, I don't know that I ought to go quite so far as this at present, for, undoubtedly, there are many benighted persons who have been in the habit of calling by no less hard names conceptions which our president tells us must be regarded with much respect. If we have four dimensions of space we may have forty dimensions, and that would be a long way beyond that which is conceivable by ordinary powers of imagination. I should, therefore, not like to draw too closely the limits as to what may be contradiction to the best established principles. Now, let us turn to a proposition which no one can possibly deny—namely, that there is a distinct sense in which man is an animal. There is not the smallest doubt of that proposition. If anybody entertains a misgiving on that point he has simply to walk through the museum close by in order to see that man has a structure and a framework which may be compared, point for point and bone for bone, with those of the lower animals. There is not the smallest doubt moreover that, as to the manner of his becoming, man is developed, step by step, in exactly the same way as they are. There is not the smallest doubt that his activities—not only his mere bodily functions but his other functions—are just as much the subjects of scientific study as are those of ants or bees. What we call the phenomena of

intelligence, for example (as to what else there may be in them, the anthropologist makes no assertion)—are phenomena following a definite causal order just as capable of scientific examination, and of being reduced to definite law, as are all those phenomena which we call physical. And just as ants form a polity and a social state, and just as these are the proper and legitimate study of the zoologist, so far as he deals with ants, so do men organise themselves into a social state, and though the province of politics is of course outside that of anthropology, yet the consideration of man, so far as his instincts lead him to construct a social economy, is a legitimate and proper part of anthropology, precisely in the same way as the study of the social state of ants is a legitimate object of zoology. So with regard to other and more subtle phenomena. It has often been disputed whether in animals there is any trace of the religious sentiment. That is a legitimate subject of dispute and of inquiry; and if it were possible for my friend Sir John Lubbock to point out to you that ants manifest such sentiments he would have made a very great and interesting discovery, and no one could doubt that the ascertainment of such a fact was completely within the province of zoology. Anthropology has nothing to do with the truth or falsehood of religion—it holds itself absolutely and entirely aloof from such questions—but the natural history of religion, and the origin and the growth of the religions entertained by the different kinds of the human race are within its proper and legitimate province. I now go a step farther, and pass to the distribution of man. Here, of course, the anthropologist is in his special region. He endeavours to ascertain how various modifications of the human stock are arranged upon the earth's surface. He looks back to the past, and inquires how far the remains of man can be traced. It is just as legitimate to ascertain how far the human race goes back in time as it is to ascertain how far the horse goes back in time; the kind of evidence that is good in the one case is good in the other; and the conclusions that are forced on us in the one case are forced on us in the other also. Finally, we come to the question of the causes of all these phenomena, which, if permissible in the case of other animals, is permissible in the animal man. Whatever evidence, whatever chain of reasoning justifies us in concluding that the horse, for example, has come into existence in a certain fashion in time, the same evidence and the same canons of logic justify us to precisely the same extent in drawing the same kind of conclusions with regard to man. And it is the business of the anthropologist to be as severe in his criticism of those matters in respect to the origin of man as it is the business of the palæontologist to be strict in regard to

the origin of the horse; but for the scientific man there is neither more nor less reason for dealing critically with the one case than with the other. Whatever evidence is satisfactory in the one case is satisfactory in the other; and if any one should travel outside the lines of scientific evidence, and endeavour either to support or oppose conclusions which are based upon distinctly scientific truths, by considerations which are not in any way based upon scientific logic or scientific truth—whether that mode of advocacy was in favour of a given position, or whether it was against it, I, occupying the chair of the Section, should, most undoubtedly, feel myself called upon to call him to order, and to tell him that he was introducing considerations with which we had no concern whatever.

I have occupied your attention for a considerable time; yet there is still one other point respecting which I should like to say a few words, because some very striking reflections arose out of it. The British Association met in Dublin twenty-one years ago, and I have taken the pains to look up what was done in regard of our subject at that period. At that time there was no anthropological department. That study had not yet differentiated itself from zoology, or anatomy, or physiology, so as to claim for itself a distinct place. Moreover, without reverting needlessly to the remarks which I placed before you some time ago, it was a very volcanic subject, and people rather liked to leave it alone. It was not until a long time subsequently that the present organisations of this Section of the Association was brought about; but it is a curious fact, that although proper anthropological subjects were at the time brought before the Geographical Section—with the proper subject of which they had nothing whatever to do—I find that even then more than half of the papers that were brought before that Section were, more or less distinctly, of an anthropological cast. It is very curious to observe what that cast was. We had systems of language—we had descriptions of savage races—we had the great question, as it then was thought, of the unity or multiplicity of the human species. These were just touched upon, but there was not an allusion in the whole of the proceedings of the Association at that time to those questions which are now to be regarded as the burning questions of anthropology. The whole tendency in the present direction was given by the publication of a single book, and that not a very large one—namely, "The Origin of Species." It was only subsequent to the publication of the ideas contained in that book that one of the most powerful instruments for the advance of anthropological knowledge—namely, the Anthropological Society of Paris—was founded. Afterwards the Anthropological Institute of this country

and the great Anthropological Society of Berlin came into existence, until it may be said that now there is not a branch of science which is represented by a larger or more active body of workers than the science of anthropology. But the whole of these workers are engaged, more or less intentionally, in providing the data for attacking the ultimate great problem, whether the ideas which Darwin has put forward in regard to the animal world are capable of being applied in the same sense and to the same extent to man. That question, I need not say, is not answered.

It is a vast and difficult question, and one for which a complete answer may possibly be looked for in the next century; but the method of inquiry is understood; and the mode in which the materials are now being accumulated bearing on that inquiry, the processes by which results are now obtained, and the observation of these phenomena lead to the belief that the problem also, some day or other, will be solved. In what sense I cannot tell you. I have my own notion about it, but the question for the future is the attainment, by scientific processes and methods, of the solution of that question. If you ask me what has been done within the last twenty-one years towards this object, or rather towards clearing the ground in the direction of obtaining a solution, I don't know that I could lay my hand upon much of a very definite character—except as to methods of investigation—save in regard to one point. I have some reason to know that about the year 1860, at any rate, there was nothing more volcanic, more shocking, more subversive of everything right and proper, than to put forward the proposition that as far as physical organisation is concerned there is less difference between man and the highest apes than there is between the highest apes and the lowest. Now my memory carries me back sufficiently to remind me that, in 1860, that question was not a pleasant one to touch on. The other day I was reading a recently-published valuable and interesting work, "L'Espèce Humaine," by a very eminent man, M. de Quatrefages. He is a gentleman who has made these questions his special study, and has written a great deal and very well about them. He has always maintained a temperate and fair position, and has been the opponent of evolutionary ideas, so that I turned with some interest to his work as giving me a record of what I could look on as the progress of opinion during the last twenty years. If he has any bias at all it is one in the opposite direction to which my own studies would lead me. I cannot quote his words, for I have not the book with me, but the substance of them is that the proposition which I have just put before you is one the truth of which no rational person

acquainted with the facts could dispute. Such is the difference which twenty years has made in that respect, and speaking in the presence of a great number of anatomists, who are quite able to decide a question of this kind, I believe that the opinion of M. de Quatrefages on the subject is one they will all be prepared to indorse. Well, it is a comfort to have got that much out of the way. The second direction in which I think great progress has been made is with respect to the processes of anthropometry, in other words, in the modes of obtaining those data which are necessary for anthropologists to reason upon. Like all other persons who have to deal with physical science, we confine ourselves to matters which can be ascertained with precision, and nothing is more remarkable than the exactness which has been introduced into the mode of ascertaining the physical qualities of man within the last twenty-five years. One cannot mention the name of Broca without the greatest gratitude; and I am quite sure that when Prof. Flower brings forward his paper on cranial measurements on Monday next you will be surprised to see what precision of method and what accuracy are now introduced, compared with what existed twenty-five years ago, into these methods of determining the physical data of man's structure. If, further, we turn to those physiological matters bearing on anthropology which have been the subject of inquiry within the last score of years, we find that there has been a vast amount of progress. I would refer you to the very remarkable collection of the data of sociology by Mr. Herbert Spencer, which contains a mass of information useful on one side or the other, in getting towards the truth. Then I would refer you to the highly interesting contributions which have been made by Prof. Max Müller and by Mr. Tylor to the natural history of religions, which is one of the most interesting chapters of anthropology. In regard to another very important topic, the development of art and the use of tools and weapons, most remarkable contributions have been made by General Lane Fox, whose museum at Bethnal Green is one of the most extraordinary exemplifications that I know of the ingenuity, and, at the same time, of the stupidity of the human race. Their ingenuity appears in their invention of a given pattern or form of weapon, and their profound stupidity in this, that having done so, they kept in the old grooves, and were thus prevented from getting beyond the primitive type of these objects and of their ornamentation. One of the most singular things in that museum is its exemplification—the wonderful tendency of the human mind when once it has got into a groove to stick there. The great object of scientific investigation is to run counter to that tendency.

Lastly, great progress has been made in the last twenty years in the direction of the discovery of the indications of man in a fossil state. My memory goes back to the time when anybody who broached the notion of the existence of fossil man would have been simply laughed at. It was held to be a canon of palæontology that man could not exist in a fossil state. I don't know why, but it was so ; and that fixed idea acted so strongly on men's minds that they shut their eyes to the plainest possible evidence. Within the last twenty years we have an astonishing accumulation of evidence of the existence of man in ages antecedent to those of which we have any historical record. What the actual date of those times was, and what their relation is to our known historical epochs, I don't think anybody is in a position to say. But it is beyond all question that man, and not only man, but what is more to the purpose, intelligent man, existed at times when the whole physical conformation of the country was totally different from that which characterises it now. Whether the evidence we now possess justifies us in going back further, or not—that we can get back as far as the epoch of the drift is, I think, beyond any rational question or doubt ; that may be regarded as something settled —but when it comes to a question as to the evidence of tracing back man further than that—and recollect drift is only the scum of the earth's surface—I must confess that to my mind the evidence is of a very dubious character.

Finally, we come to the very interesting question—as to whether, with such evidence of the existence of man in those times as we have before us, it is possible to trace in that brief history any evidence of the gradual modification from a human type somewhat different from that which now exists to that which is met with at present. I must confess that my opinion remains exactly what it was some eighteen years ago when I published a little book which I was very sorry to hear my friend, Prof. Flower, allude to yesterday, because I had hoped that it would have been forgotten amongst the greater scandals of subsequent times. I did there put forward the opinion that what is known as the Neanderthal skull is, of human remains that which presents the most marked and definite characteristics of a lower type—using the language in the same sense as we would use it in other branches of zoology. I believe it to belong to the lowest form of human being of which we have any knowledge, and we know from the remains accompanying that human being, that as far as all fundamental points of structure were concerned, he was as much a man —could wear boots just as easily—as any of us, so that I think the question remains pretty much where it was. I don't know that there

is any reason for doubting that the men who existed at that day were in all essential respects similar to the men who exist now. But I must point out to you that this conviction is by no means inconsistent with the doctrine of evolution. The horse, which existed at that time, was in all essential respects identical with the horse which exists now. But we happen to know that going back further in time the horse presents us with a series of modifications by which it can be traced back from an earlier type. Therefore it must be deemed possible that man is in the same position, although the facts we have before us with respect to him tell in neither one way nor the other. I have now nothing more to do than to thank you for the great kindness and attention with which you have listened to these informal remarks.

XVI

ON THE CLASSIFICATION AND THE DISTRIBUTION OF THE CRAYFISHES

Proceedings of the Scientific Meetings of the Zoological Society of London, 1878. *pp.* 752–788. (*Read June 4th*, 1878.)

I. INTRODUCTION

THE dismemberment of the genus *Astacus* of the older naturalists, down to the time of Fabricius, was commenced by Leach, who separated the Norway Lobster as the type of a new genus, *Nephrops*[1].

Milne-Edwards advanced a step further by establishing the genus *Homarus* for the Lobsters, and leaving only the freshwater *Astaci*, or the proper Crayfishes, in *Astacus*.[2]

The later proposal of Leach, to use *Astacus* for the Lobsters, and to give a new generic name (*Potamobius*) to the freshwater Crayfishes, would have had the advantage of retaining the primitive signification of ἀστακός. But *Potamobius* had already been used in another sense; and the change introduced by Milne-Edwards is so

[1] Leach, Trans. Linn. Soc. xi. 344.

[2] 'Histoire Naturelle des Crustacés,' 1837.

generally adopted that it would be confusing to attempt any further alteration.

Guérin[1] next proposed to distinguish the *Astacus madagascariensis* of Audouin and Milne-Edwards, as *Astacoides*, from the other Crayfishes; and Erichson, in his valuable Monograph of the group,[2] adopts *Astacoides* for the Madagascar and some of the Australian forms, and establishes the new genera *Cambarus*, *Chæraps*, and *Engæus*. In *Cambarus* and *Chæraps* the number of the branchiæ is taken into account as an important generic character.

In 1842[3] Mr. Adam White described some Crayfish from New Zealand, for which he constituted a new genus, *Paranephrops*, under the impression that the New Zealand form approximated to the genus *Nephrops*. Mr. Wood-Mason[4] has since "denied the existence of any special relationship between the New Zealand species of freshwater *Astacidæ* and the marine genus *Nephrops*;" and "as the species referred to *Paranephrops* differed less from [some of] those of *Astacoides* than these latter did from one another, and as, moreover, the latter name had the priority, he proposed provisionally to refer the New Zealand species of *Astacidæ* to it."

Mr. Wood-Mason is unquestionably right both in denying any special relationship between *Paranephrops* and *Nephrops*, and in asserting that the New Zealand Crayfish differ less from some of the species of the genus *Astacoides*, as its limits are at present understood, than these do from one another. But I shall have occasion to show that the type of the genus *Astacoides*, the Madagascar Crayfish, differs so widely from the other Crayfishes of the southern hemisphere, that the latter cannot be included in the same genus; while *Paranephrops* is sufficiently different from the Australian and Tasmanian Crayfishes to render its recognition as a distinct generic type desirable.[5]

The distribution of the Crayfishes, so far as it is hitherto ascertained, is not a little remarkable. *Astacus fluviatilis* occurs in various parts of England and in Ireland; but I cannot find any record of it in Scotland. Dr. M'Intosh, who has been kind enough to look into this point in aid of my inquiries, assures me that Crayfishes are not indigenous to that part of Britain, that they do not exist in the Tweed and the Teviot, and that an attempt to introduce them into

[1] Revue Zoologique, 1839.

[2] "Uebersicht d. Gattung Astacus," Archiv für Naturgeschichte, Bd. 6.

[3] Gray's 'Zoological Miscellany.' See also Dieffenbach's 'New Zealand,' 1843, vol. ii. p. 267.

[4] Proc. Asiat. Soc. Bengal, 1876, p. 4.

[5] See on this subject the remarks of Mr. Miers, "Note on the genera *Astacoides* and *Paranephrops*" (Ann. & Mag. Nat. Hist. ser. 4, vol. xviii. 1876).

the island of Mull failed; they were placed in various streams, but none were ever seen again. Even in England, Crayfishes appear to be restricted to certain rivers. They abound, for example, in the Thames; but I cannot hear of any in the Cam or the Ouse, though their absence in the latter rivers cannot be ascribed to any want of calcareous matter in the districts through which those rivers flow.

Astacus fluviatilis, however, extends all over the western half of Europe, as far south as the Pyrenees and the northern shores of the Mediterranean; while, eastward, it reaches Sicily, Northern Greece, and the western shores of the Black Sea. In Spain there appears to be no doubt that it occurs about Barcelona; but whether it is found in the rest of the Spanish peninsula is uncertain.[1]

Northwards and eastwards, *Astacus fluviatilis* extends to Sweden and the Baltic provinces of Russia, and through Western Russia, by the basins of the Dniester and the Bug, to the Black Sea.

Over this vast area, marked local varieties appear to be not uncommon; and most authors agree to regard a Crayfish which occurs in Southern Europe, France, Switzerland, and Germany, and which is known in the latter country as the "Steinkrebs," as a distinct species, *Astacus torrentium* or *A. saxatilis*.[2]

Eastward of the region inhabited by *Astacus fluviatilis*, from the Arctic to the Black and Caspian Seas, another species, *A. leptodactylus*, ranges, associated with the allied but possibly distinct forms *A. pachypus* and *A. angulosus*, in the southern part of the area; and it is remarkable that these Crayfishes not only frequent the rivers which debouch into the Black Sea and the Caspian, but are said to thrive in the salt waters of those seas.

[1] See Gerstfeldt, 'Ueber die Flusskrebse Europa's' (Mém. presentés à l'Acad. Imp. des Sciences de St. Petersbourg, 1859, p. 587). As far back as 1675, Sachs à Lewenheimb wrote:—"Sic in Hispaniâ licet flumina, negant inveniri ibi *Cancros fluviatiles*, contrà in Galliâ frequentissimi, item in Pannoniâ, in Helvetiâ, in Germaniâ; etiam in fluviis Americanis inveniri referunt navigatores. In fluvio Lydiæ Haly cancros invenit Busbequius, Ep. Turc. i. p. 89." But were these Lydian "cancri" crayfishes or fluviatile crabs?

[2] In 1560, Gesner was acquainted with this distinction:—"Astacus fluviatilis talis apud Helvetios et Germanos est, major silicet et simpliciter dictus *Krebs* vel *Edelkrebs*; eo enim minor est, et colore diversus qui saxatilis cognominatur *Steinkrebs*." ('Nomenclator Aquatilium,' p. 374). Heller ('Die Crustaceen des südlichen Europa,' p. 217) refers our English Crayfish to this species; but no specimens I have seen agree with his diagnosis. Whether there is any difference between *A. saxatilis* and the Crayfishes which have been named *A. pallipes* and *A. fontinalis* by Lereboullet and Carbonnier; and whether our English Crayfish is more similar to these than to the form which is commonly known as *A. fluviatilis* on the Continent, is more than I am able to say at present. A critical comparison of large series of specimens from different localities would probably yield results of great interest to the theory of the origin of species.

No Crayfishes are known in the Ob, Jenisei, Lena, or other rivers which flow into the Arctic Ocean;[1] but the Amur has one or two species (*A dauricus*). There is a species in Japan (*A. japonicus*); and Dr. Hagen[2] enumerates no fewer than six species from British Columbia, Oregon, and California.

East of the Sierra Nevada, all the Crayfishes at present known belong to the genus *Cambarus*, of which Dr. Hagen distinguishes as many as thirty-two species. They extend from the Great Lakes to Mexico, Guatemala, Cuba, and probably other of the West India Islands. Sloane, in his 'Natural History of Jamaica' (vol. ii. p. 271) describes two species in that island. According to the figure, one of these attains a length of 12 inches.

No Crayfishes are known to occur in the whole continent of Africa, in Syria, the Euphrates valley, Persia, Hindostan, and India beyond the Ganges, nor in China as far as the Corea, nor in the Philippines, nor in any island of the Malay or Papuan archipelagos.[3] The late Prof. Agassiz, though he sought for Crayfishes in the Amazons, could find none. Two species from Southern Brazil have been described by Dr. von Martens[4] as *Astacus brasiliensis* and *A.*

[1] Kessler, "Die russischen Flusskrebse" (Bull. de la Soc. Imp. des Nat. de Moscou, 1874).

[2] 'Monograph of the North-American Astacidæ,' Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College, 1870.

[3] I have been favoured by Sir Henry Barkly with the opportunity of examining specimens of two kinds of "Cammarons," or so-called Crayfishes, from the rivers of Mauritius. They are large Prawns.

I must confess myself to be in a state of hopeless perplexity respecting the Crayfish or Lobster which is said to occur at the Cape of Good Hope, *Cancer* (*Astacus*) *capensis* of Herbst. At the beginning of his description ('Naturgeschichte der Krabben und Krebse,' Band ii. p. 49) Herbst says:—"Dieser schöne Krebs hält sich auf den Kap in solchen Flüssen auf, die sich auf den Bergen befinden;" and at the end he states, "die Füsse haben insgesammt scheerenförmige Spitzen, da bey dem gemeinen Flusskrebs nur die ersten zwey Paare dergleichen haben." Moreover, the diagnosis runs, "pedibus omnibus cheliferis." It is impossible to suppose that Herbst should have made a mistake on such a point as this; and therefore it must be concluded that his *Cancer capensis* is neither a Crayfish nor a Lobster, and that, unless he was wrongly informed, it is an inhabitant of fresh water.

Milne-Edwards ('Hist. Nat. des Crustacés,' ii. p. 335) identifies his *Homarus capensis* with the *Cancer capensis* of Herbst; but, as it is stated in the definition of the genus *Homarus* (*l. c.* p. 333) that the Lobsters "ne se trouvent que dans la mer," and as *Homarus* has only three pairs of chelate limbs, the identification presents difficulties. Krauss ('Südafrikanische Crustaceen,' p. 54), under the head of "*Homarus capensis*," refers to Herbst and Milne-Edwards, and, apparently on the authority of the former, merely says:—"In den Bergflüssen des Kaplandes. Ich habe ihn in Natal nie geschen." Elsewhere (p. 20) he gives "*Thelphusa perlata* and *T. depressa* and *Homarus capensis*" as the only South-African freshwater Thoracostraca.

[4] "Südbrasilische Süss- und Brackwasser-Crustaceen," Archiv für Naturgeschichte, 1869.

pilimanus; but Von Martens recognises the affinity of these forms with the *Astacoides* of Erichson.

Several species of *Paranephrops* have been described from New Zealand; and the Fijian Crayfish belongs to the same genus.

Crayfishes occur all over Australia; and the species have been referred to the genera *Astacoides* and *Chæraps*. The only Tasmanian species which have been described constitute the genus *Engæus* of Erichson.

Thus it appears, from what is already published on this subject:—

1. That the Crayfishes of the northern hemisphere are generically distinct from those of the southern hemisphere.

2. That the American Crayfishes, east of the Sierra Nevada, are generically distinct from those west of that range, as well as from the South American species; and that, while the western North American Crayfishes belong to the same genus as those of the Old World, the South American forms are more closely allied with those of Madagascar and Australia.

3. That the New Zealand species are distinct from the Australian forms; and that the latter are to be placed in the same genus as the Madagascar and South American species.

4. That there is a negative fact of distribution, not to be accounted for by any apparent difference of climate or other physical conditions —namely, the entire absence of Crayfishes in Equatorial South America, Africa, and the rest of the Old World south of the northern escarpment of the great Asiatic highlands.

The problem thus offered is one of the most remarkable among the many presented by the facts of Geographical Distribution; and it appeared to me that one of the first steps towards attempting its solution was to obtain some more definite conception, than is furnished by extant descriptions, of the actual amount of resemblance and difference between the Crayfishes which are found in the different areas of distribution.

For the most part the Crayfishes are so similar in their general structure, that the characters by which the genera have been distinguished are almost trivial. Erichson, however, has drawn attention to the diminution of the number of the branchiæ in *Cambarus* and *Astacus*, and to an important difference in the structure of those of *Engæus*; and Hagen has pointed out some important peculiarities of these organs in *Cambarus*; while the remarkable fact, that the appendages of the first somite of the abdomen are absent in many of the Crayfishes of the southern hemisphere, has been duly noted by Erichson and several other zoologists.

Having recently had occasion to make a careful reexamination of the structure of *Astacus fluviatilis*, I found two minute filaments attached to the epimera of the penultimate and antepenultimate thoracic somites. The structure and the position of those filaments led me to suspect that they must be rudimentary branchiæ;[1] and as the Australian Crayfishes appeared to me to be, on the whole, less specialised forms than the European species, I thought that I should probably find in them fully-formed functional branchiæ occupying the place of these rudiments. Through the kindness of my friend and former pupil, Mr. J. Wood-Mason, a specimen of "*Astacoides*" *franklini* was placed at my disposal; and on examination, I not only found the functional branchiæ I sought, but discovered a number of other interesting differences between the respiratory organs of this Crayfish and those of *Astacus*.

Following up the line of inquiry thus suggested, I have examined examples of all the chief forms of Crayfishes at present known, with the result of establishing some remarkable parallel relations between the morphology and the distribution of these animals.

In order to make these points clear, I must premise a fuller and more precise description of the branchial apparatus of the common Crayfish than has yet been given, in order that it may serve as a standard of comparison for the branchiæ of the other Crayfishes.

II. The Modifications of the Branchiæ in the Crayfishes.

The Branchiæ of Astacus fluviatilis.

When the branchiostegite of a Crayfish is removed, seven branchiæ are seen, running from the base towards the apex of the branchial cavity, parallel with one another, and disposed in curved lines, which are concave forwards and convex backwards. The length of the branchiæ gradually increases from the first to the sixth; the seventh ascends as high as the sixth, but is rather shorter, in consequence of the attachment of its base lying at a higher level.

In each of the six anterior branchiæ, a *basal portion*, a *stem*, an expanded *lamina*, and an *apical plume* may be distinguished. The *basal portion* (fig. 1, 1, B) is broad, with a convex posterior and

[1] I have met with no allusion to these structures, unless the following passage in Brandt's and Ratzeburg's description of the Crayfish ('Med.-Zoologie,' ii. p. 61) refers to them:—"Ueber jeder der obersten Kiemen der beiden mittlern Fusspaare steht etwa 1‴ entfernt ein kleiner fädenförmiger, unten breiterer, bärtelähnlicher Theil." I do not quite see the applicability of "unten breiterer," unless "unten" applies to the attached ends of the filaments; but in other respects the description fits the rudimentary branchiæ very well.

inferior free edge, beset with long setæ; and it is articulated by its truncated anterior end with the coxopodite of one or other of the

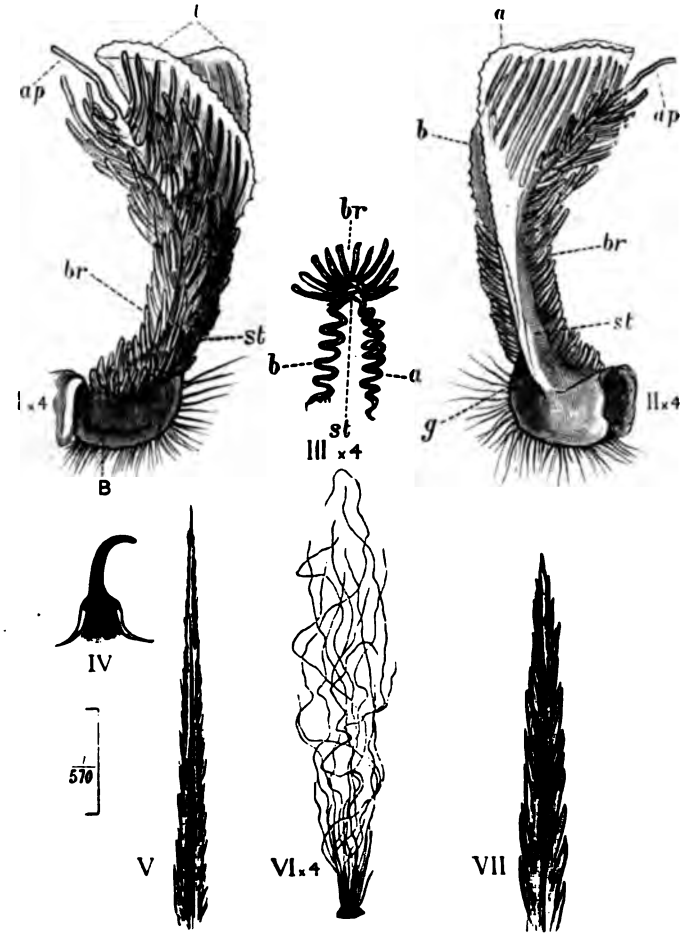

FIG. 1.—*Astacus fluviatilis.*

I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side (× 4): B, the basal portion; *st*, the stem; *l*, the lamina; *br*, the branchial filaments; *a p*, the apical plume. II. The inner face of the same podobranchia (× 4): the letters as before, except *g*, the decurrent fringe, continued from the inner lobe of the lamina. III. A transverse section of the podobranchia, taken a little above the level of *b* in II. (× 4): *a*, the inner lobe of the lamina; *b*, its outer lobe; *st*, the stem; *br*, the branchial filaments. IV. One of the hooks of the lamina; and V. The extremity of one of the setæ of the base of the podobranchia: the vertical line indicates the scale to which these figures are drawn, and represents $\frac{1}{570}$ of an inch. VI. The coxopoditic setæ of the same limb (× 4). VII. The free end of one of these setæ, magnified to the same degree as IV. and V.

thoracic limbs, from the second maxillipede to the penultimate ambulatory limb inclusively. I shall therefore term these gills

podobranchiæ. A fold of the integument rises over the outer face of the basal portion of the branchia, which is freely movable, inwards and outwards, upon its articulation.

The basal portion of the branchia curves slightly upwards, and is continued into the comparatively narrow *stem* (fig. 1, *st*), which bends up at right angles to the base, and lies nearly parallel with the inner wall of the branchial chamber. Rather beyond the middle of its length, the stem expands into the broad *lamina* (fig. 1, *l*), the two lobes of which are folded together like the leaves of a partly open book, their free rounded edges being turned backwards and the uniting fold forwards. The lamina of each branchia, from the second to the sixth, is received between the lobes of the lamina of that which precedes it, and, from the first to the fifth, receives the lamina of the branchia which follows it.

The edges of the laminæ are beset with minute hooked spines, seated upon low tubercles (fig. 1, IV.), and are flat; but, a short distance within the edge, each lamina is folded longitudinally in such a manner as to give rise to ten or twelve plaits. From the mode of their formation, these plaits or folds are, of course, as distinctly marked on the outer as on the inner faces of the laminæ (fig. 1, III.). Small elevations, terminated by minute hooked setæ, like those on the edges of the laminæ, are observable on both faces, particularly on the ridges.

The inner lobe of the lamina is continued down the stem as a decurrent gradually narrowing fringe, which terminates on the inner face of the basal portion (fig. 1, II. *g*). The outer lobe ends more abruptly, in a thin ridge which lies external and posterior to the last. Between this ridge and the fringe there is a longitudinal groove, which occupies the inner and posterior face of the stem.

A short distance from the upper edge of the lamina, and proceeding, as it were, from the anterior face of the median fold of the latter, the *apical plume* (fig. 1, I. *a p*) is given off. At its base this is beset with cylindrical branchial filaments; but at its free extremity it becomes simple and filiform; at its attached extremity, it passes into the stem of the gill, of which it is seen to be the direct continuation. The whole of the outer and anterior face of the stem, as far as the basal fold, is beset with branchial filaments, of which those in the region of the lamina are the longest, while towards the base they are shorter and more closely set.

Close to the attachment of the podobranchia, the upper surface of the coxopodites presents a rounded elevation, from which a great number of long, flexible and tortuous setæ proceed (fig. 1, VI.). When

undisturbed, they ascend vertically between the gills on the sides of the branchial chamber. The apex of each of these *coxopoditic setæ* is acute; and at a short distance from its extremity it is beset with numerous short foliaceous scales, which gives it the aspect of a minute catkin (fig. 1, VII.). Further down these scales become more widely separated, and at length disappear, the base of the seta being smooth. A canal traverses the whole length of the seta.

These bundles of setæ were regarded as branchiæ by Brandt and Ratzeburg; but they certainly have no direct relation to the respiratory function. They may aid in keeping parasites out of the branchial chamber.

The setæ which fringe the base of the podobranchia are straight, stiff, hollow, and composed of a cylindrical basal portion, and an acuminated acicular terminal part, which often appears articulated with the foregoing; the junction of the two is marked by an inflexion of the wall of the seta. The acicular part (fig. 1, V.) is fringed with minute pointed scales, which, in the setæ of the anterior part of the base, pass into long lateral processes, and give the seta a penniform appearance. None of these setæ are hooked at the apex.

The only differences, except those of size, which are observable in the six podobranchiæ, are, that the external lobe of the lamina, which is not nearly so large as the internal, in the hindermost branchia increases in relative size, until, in the most anterior branchia it becomes larger than the internal lobe. The penniform setæ are more numerous on the bases of the anterior podobranchiæ.

The first maxillipede is said, and, in a physiological sense, rightly, to possess no branchia; but it is provided with an appendage (fig. 2, A, C) which is undoubtedly the homologue of the podobranchia of the other thoracic limbs. This is a soft membranous plate, which broadens at its upper extremity, and sends a short process downwards beyond its articulation with the coxopodite of the maxillipede. The plate is slightly folded upon itself longitudinally, but in such a manner that it is concave forwards instead of backwards. It bears no branchial papillæ, and has no longitudinal plaits; but, on its posterior face and along its inner edge, it presents hooked tubercles, like those of the laminæ of the podobranchiæ. It is obvious that this structure, which lies immediately behind and parallel with the scaphognathite of the second maxilla (but, as I have ascertained, does not share its function of scooping the water out of the branchial cavity [1]), is a

[1] If the branchiostegite of a living Crayfish is carefully removed, the rapid rhythmical motion of the scaphognathite is readily seen; but the modified podobranchia of the first maxillipede remains quiescent.

modified podobranchia, reduced, as it were, to the part which, in the other podobranchiæ, is represented by the base, stem, and lamina.

Thus every thoracic limb, except the last, is provided with the representative of a podobranchia—though, in the case of the first maxillipede, this structure, if it plays any part in the respiratory process, does so simply in virtue of its thin and soft texture, and

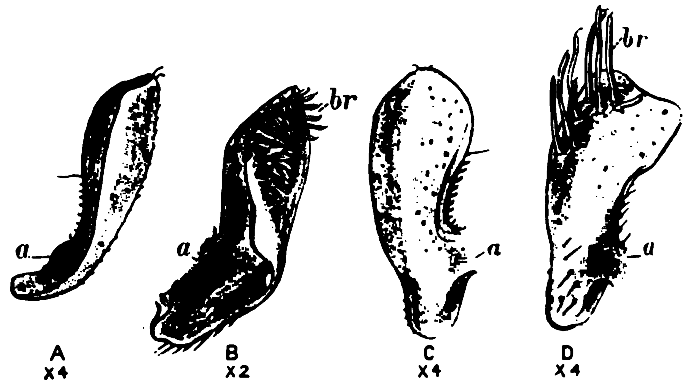

FIG. 2.—A. The podobranchia (epipodite) of the first maxillipede of *Astacus fluviatilis*, viewed from the outer side (× 4). B. The podobranchia of the first maxillipede of *Astacoides madagascariensis*, outer side (× 2): *br*, branchial filaments. C. The podobranchia (epipodite) of the first maxillipede of *Astacus fluviatilis*, viewed from behind (× 4). D. The podobranchia of the first maxillipede of *Parastacus brasiliensis*, from behind (× 4); *br*, branchial filaments. In each figure *a* marks the pedicle by which the more or less modified podobranchia is attached to the coxopodite.

not by means of any special branchial filaments. The podobranchia of the first thoracic appendage is, in fact, reduced to a mere *epipodite*.

When the podobranchiæ are removed, six other gills come into view. They are attached (fig. 3, *arb*) to the flexible membrane which unites the coxopodites of all the thoracic limbs to the thorax, save the first and last, and may be termed *anterior arthrobranchiæ*. Like the foregoing, they are disposed vertically, and increase in size from the first, which belongs to the second maxillipede and is hidden behind the epipodite of the first maxillipede, to the last. The apex of each of these gills is exactly like the apical plume of one of the podobranchiæ; and the branchial filaments are set upon the outer and anterior face of the stem in the same way. The inner face is flat and free from filaments; and there is no trace of a lamina or of a basal dilatation.

Above and behind these, more directly above in the posterior, more behind in the anterior limbs (fig. 3, *arb*), are five other branchiæ of similar character, attached to the arthrodial membranes of the third maxillipede and the anterior four ambulatory limbs. These may be termed the *posterior arthrobranchiæ*.

After the removal of all these functional branchiæ, there will be found, immediately above the bases of the penultimate and antepenultimate thoracic limbs (fig. 3, 12 *plb*, 13 *plb*), two minute filamentous processes, the longer of which was not more than one sixth of an inch in length in any specimen I have examined, while both are so delicate as to be invisible except under a simple lens. The posterior of these is the larger: it has the structure of an ordinary branchial filament, with a somewhat swollen base, which is attached to the margins of a foramen in the lower part of the epimeron of the penultimate thoracic somite, just below a transverse depression which separates this from the upper part of the epimeron. The position of this filament is sometimes vertical, but more frequently horizontal. The anterior filament is sometimes a mere papilla; it is attached to the margins of a small foramen which occupies a similar position in the antepenultimate epimeron—namely, close to the anterior edge and just below the transverse depression. These are two rudimentary gills, of the same order as that next to be described.

The seventh, and most posterior branchia of those which become visible when the brachiostegite is removed (fig. 3, 14 *plb*), has yet to be considered. It resembles one of the arthrobranchiæ in all essential characters, but it is not attached to the arthrodial membrane; on the

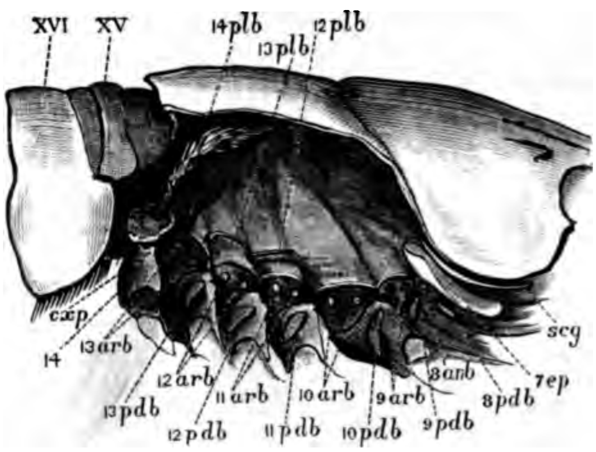

FIG. 3.—*Astacus fluviatilis.*

The branchiostegite, all the podobranchiæ, except the epipodite of the first maxillipede, and all the arthrobranchiæ of the right side are removed (× 4).

contrary, the base of its stem is fixed to the margins of a circular aperture situated close to the edge of a peculiar shield-shaped plate, the posterior and outer surface of which is covered with strong setæ. Immediately behind and below the attachment of the gill there is an oval space, occupied by a soft and flexible portion of the cuticle, like

a tympanic membrane. By its lower margin this plate furnishes an articular surface to the outer condyle of the coxopodite of the last thoracic limb, while its anterior and upper angle, bending sharply upwards, passes into a curved prolongation, which extends upwards and backwards in the soft integument of the flank, and articulates with a slender process of somewhat similar form sent forward from the first abdominal somite. Internally this shield-shaped branchiferous plate is continuous with the sternum of the last thoracic somite. It is obvious that this plate, with its anterior process, represents the epimeron of the last thoracic somite, which is thus adherent to the penultimate somite only by the slender anterior and superior process and the soft integument. Hence, the last thoracic somite moves easily upon its predecessor, though, in strictness, the usual statement that the last thoracic somite in *Astacus* is "free" is not altogether exact.

It follows from this determination of the nature of the shield-shaped plate, that the gill which it bears is attached to the epimeron, or side-wall, of the last thoracic somite; and it may be termed a *pleurobranchia*. The similarly attached filaments (12 *plb* and 13 *plb*) represent reduced or rudimentary pleurobranchiæ.

We may suppose that the total number of branchiæ which a thoracic somite can possess is eight, four on each side, namely:—one podobranchia, connected with the coxopodite of the appendage; two arthrobranchiæ, fixed to the articular membrane; and one pleurobranchia, attached to the epimeron. And if four places for branchiæ are assigned to each somite, the extent to which the hypothetically complete scheme or formula is actually filled up will be readily seen, and the branchial arrangements of different Crayfishes will be easily compared.

The Branchial formula of Astacus fluviatilis[1].

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.	
		Anterior.	Posterior.		
VII............	o (ep)	o	o	o	= o (ep)
VIII............	1	1	o	o	= 2
IX............	1	1	1	o	= 3
X............	1	1	1	o	= 3
XI............	1	1	1	o	= 3
XII............	1	1	1	*r*	= 3 + *r*
XIII............	1	1	1	*r*	= 3 + *r*
XIV............	o	o	o	1	= 1
	6 + ep	+ 6	+ 5	+ 1 + 2*r*	= 18 + ep + 2*r*.

[1] In this, as in all other cases, it is to be understood that the branchial formula gives the branchiæ of only one side of the body, and that the total number of branchiæ is therefore double that given in the formula.

"ep" here signifies a podobranchia which has lost its branchial filaments and become completely metamorphosed into an epipodite, while *r* indicates that a rudiment of a branchia exists.

It will be observed that, in this species of Crayfish, no somite possesses its hypothetically full complement of branchiæ except XII. and XIII.; and even in them the pleurobranchiæ are rudimentary. The representatives of eleven possible branchiæ are altogether wanting.

2. *The Branchiæ of* Cambarus.

The principal distinction between this genus and *Astacus*, as it was established by Erichson, lies in the absence of the single pleurobranchia of the latter, and the consequent reduction of the number of the branchiæ to seventeen on each side.

In his elaborate monograph of the genus, Dr. Hagen observes, "But there is also another difference, not before noticed.[1] In *Astacus* each pair of gills, except the single one on the fifth set of legs, has a broad deeply-folded membrane, closely fixed behind the most external gill-lobe. In *Cambarus*, this membrane is always wanting in the gills of the fourth pair of legs, but exists, as in *Astacus*, in all the others.

"In the true *Astacus*, all the gills with a folded membrane behind have a basal external bundle of shorter but broader and irregularly placed gill-tubes; these are never to be found in *Cambarus*."

In a species of *Cambarus* from Guatemala, of which a number of specimens have been presented to the British Museum by Mr. Salvin,[2] I find Dr. Hagen's first remark fully borne out. The last podobranchia is devoid of even a trace of a lamina; in the five which precede it, on the other hand, the lamina is very large, and folded into two longitudinally plaited lobes, as in *Astacus*. The edges and the surfaces of the laminæ present tubercles, which are more prominent than in *Astacus*, and bear similar hooked spines.

The inner decurrent prolongation of the lamina is wider than in *Astacus*, particularly in the anterior podobranchiæ. It is also beset with hooked setæ mounted on low tubercles.

[1] Dr. Hagen appears to have overlooked De Haan's definition of the distinctive characters of the American Crayfishes known to him:—

"Branchiæ 17; nulla supra pedes quintos; *externæ supra quartos tantum e tubulis liberis*, externæ supra sequentes infra e tubulis, supra e laminis tuberculatis compositæ" ('Fauna Japonica,' Crustacea, p. 164).

[2] Mr. Salvin informs me that they were obtained in a river near Coban, in Vera Paz, at an elevation of about 4300 feet above the sea.

The setæ of the upper part of the base are relatively shorter. As in *Astacus*, their apices are straight and not hooked.

The coxopodites bear bundles of twisted setæ, which are similar to those of *Astacus*, but are more obtusely pointed.

The arthrobranchiæ are similar in number and in form to those of *Astacus*. Those of the posterior series are proportionately larger.

I cannot discover a trace of the hindermost pleurobranchia, nor of the rudiments of the anterior ones, in this species; but it is not improbable that they may be discovered in larger forms.

The modified podobranchia (epipodite) of the first maxillipede is soft, and folded longitudinally in such a manner as to present a broad and shallow anterior groove. It bears no branchial papillæ, nor any setæ; but there are a few short hooks here and there.

The Branchial formula of Cambarus.

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleuro-branchiæ.		
VII............	0 (ep)	0	0	0	=	0 (ep)
VIII............	1	1	0	0	=	2
IX............	1	1	1	0	=	3
X............	1	1	1	0	=	3
XI............	1	1	1	0	=	3
XII............	1	1	1	0	=	3
XIII............	1	1	1	0	=	3
XIV............	0	0	0	0	=	0
	6 + ep	+ 6	+ 5	+ 0	=	17 + ep.

In comparison with *Astacus*, there is obviously a reduction of the branchial system, arising from the complete disappearance of all the pleurobranchiæ in *Cambarus*.

3. *The Branchiæ of* Astacopsis[1] franklinii.

When the branchiostegite is removed, seven branchiæ are seen, having the general appearance and disposition of those of *Astacus*; and, as in *Astacus*, the six anterior are podobranchiæ, attached to the coxopodite of the second maxillipede and the five following appendages, while the seventh is a pleurobranchia, fixed to the epimeron of the last thoracic somite. There is also an anterior series of six arthrobranchiæ and a posterior series of five (p. 289, fig. 4, *arb*), disposed

[1] Since, as will be shown below, those Australian Crayfishes which neither belong to *Chæraps* nor to *Engæus* are distinct from *Astacoides*, as represented by the Madagascar species I propose to apply the generic name of *Astacopsis* to them.

as in *Astacus*. But instead of the two rudimentary pleurobranchiæ borne by the twelfth and thirteenth somites, in *Astacus*, there are three perfect branchiæ attached to the eleventh, twelfth, and thirteenth somites (fig. 4, 11–13 *plb*), in positions which, in the case of the two latter, exactly correspond with those of the rudimentary pleurobranchiæ of *Astacus*.

The pleurobranchiæ and the arthrobranchiæ are very similar to those of *Astacus*; but the inner surface of the stem is channelled by a sort of groove, the edges of which are pretty sharp. I could find

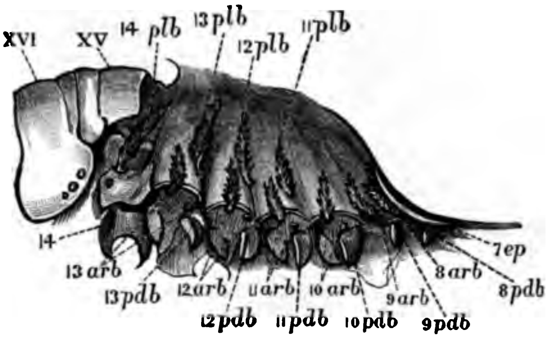

FIG. 4.—*Astacopsis franklinii.*

The branchiostegite, all the podobranchiæ, except that of the first maxillipede, and all the anterior arthrobranchiæ, except the first, of the right side are removed (× 2).

scg, scaphognathite (not shown in fig. 4); 7 *ep*, the podobranchia of the first maxillipede; 8 *pdb* to 13 *pdb*, the other podobranchiæ; 8 *arb* to 13 *arb*, the arthrobranchiæ or their attachments to the arthrodial membranes of the second and following thoracic appendages; 11 *plb* to 14 *plb*, the pleurobranchiæ; 14, the coxopodite of the hindermost ambulatory limb; *cxp*, the coxopoditic setæ of that limb in *Astacus*.

no hooks, nor spines, nor hooked papillæ on any part of these branchiæ.

The podobranchiæ (fig. 5, I, II, III) resemble those of *Astacus* in their general form; but the basal portion is relatively larger and the stem stouter, while, at first sight, the lamina appears to be altogether wanting. Close examination, however, shows that the apex of the branchia is distinguishable into an apical plume and a lamellar appendage, but that the latter is relatively very small; in fact, it is a mere outgrowth of the inner wall of the stem, and is neither bilobed nor plaited. Moreover its surface is beset with numerous filamentous prolongations, which are altogether similar to ordinary branchial filaments, except that the extremity of each, instead of being smooth and rounded, is provided with a short recurved hook-like seta (fig. 5, II *a*, IV). The groove on the inner or posterior face of the stem is broader than in *Astacus*. It is bounded on the inner side by a decurrent fringe, which runs down

on to the base and stops there, as in the foregoing genera (fig. 5, II). This fringe is provided with long slender curved setæ, each beset with imbricated scales and terminated by a recurved hook (fig. 5, V). The external ridge is wider than in *Astacus*, and is provided with

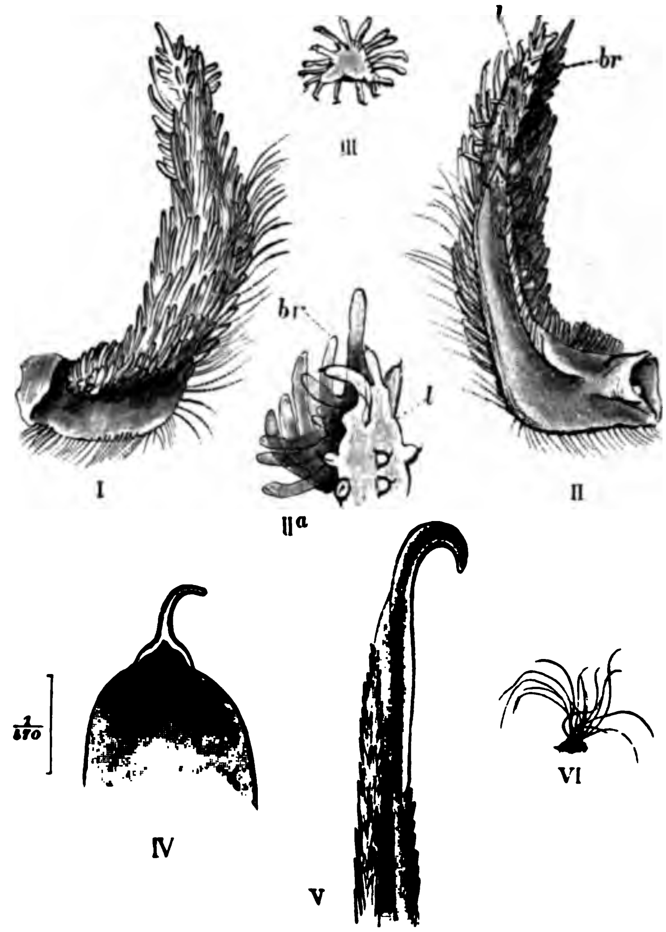

FIG. 5.—*Astacopsis franklinii.*

I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side (× 3½). II. The inner face of the same podobranchia : *br*, branchial filaments ; *l*, rudimentary lamina. II *a*. The apex of the same, more highly magnified. III. A transverse section of the podobranchia at about the junction of its middle and upper thirds. IV. The extremity of one of the hooked filaments ; and V, that of one of the hooked setæ. In these two figures the vertical line represents $\frac{1}{170}$ of an inch magnified to the same extent. VI. The coxopoditic setæ (× 3½).

similar hooked setæ. It may be said, in fact, that the whole lower half of the posterior margin of the stem in *Astacopsis* has the character of the posterior margin of the base, while in *Astacus* there is a sharp demarcation between the base and the stem.

In principle, therefore, the podobranchiæ of *Astacopsis* are similar to those of *Astacus*; and the main difference between the two is that the lamina in the former is represented by a slight expansion of the stem, which is neither bilobed nor plaited, while its surface is covered with cylindrical filaments terminated by hooked spines. In *Astacus*, as in *Cambarus*, on the other hand, the lamina is large, bilobed, plaited, and the place of the filaments is taken by mere papillæ terminated by similar hooks. Moreover, in *Astacus* and *Cambarus* the setæ of the base are not hooked.

The appendage of the first maxillipede is similar to that of *Astacus* in form; but on the outer surface of the outer lobe there are sixteen or eighteen short branchial papillæ, some of which, but apparently not all, are terminated by hooks; in fact, except in size, they quite resemble the filaments of the other branchiæ.

In this Crayfish, therefore, the first podobranchia is not reduced to a mere epipodite, but retains true branchial characters in the scanty respiratory filaments of its outer lobe.

There are only small tufts of short, straight or slightly curved setæ in the position of the bundles of long coiled coxopoditic setæ of *Astacus* and *Cambarus* (fig. 5, VI).

The Branchial formula of Astacopsis.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.		
		Anterior.	Posterior.			
VII	0 (ep *r*)	0	0	0	=	0 (ep *r*)
VIII	1	1	0	0	=	2
IX	1	1	1	0	=	3
X	1	1	1	0	=	3
XI	1	1	1	1	=	4
XII	1	1	1	1	=	4
XIII	1	1	1	1	=	4
XIV	0	0	0	1	=	1
	6 + ep *r* +	6 +	5 +	4	=	21 + ep *r*.

Thus *Astacopsis* presents a much nearer approximation to the hypothetically complete branchial formula than *Astacus*, inasmuch as the epipodite of the first maxillipede is an imperfect branchia, and there are four complete pleurobranchiæ: only the hindermost podobranchia, the first and last anterior arthrobranchiæ, the first two and the last posterior arthrobranchiæ, and the first four pleurobranchiæ are wanting. In fact, this is the most complete branchial formula with which I am at present acquainted, among the podophthalmous Crustacea.

4. *The Branchiæ of* Chæraps (?).

I have examined a single specimen of a species attributed to this genus, from the Yarra-Yarra river, in the collection of the British Museum.[1]

The second maxillipede and the five following thoracic limbs bear podobranchiæ, which increase in length from the first to the last, and have a close general resemblance to those of *Astacopsis*; but they differ in the production of the upper part of the anterior lip of the groove of the stem into a broad limb or ala, wider at the upper end than below, which must not be confounded with the lamina oı *Astacus*, as it corresponds only with part of the inner lobe and the decurrent fringe in that genus (fig. 6, I, II, III *al*). Both faces, as well as the free posterior margin of this fringe, are beset with cylindrical branchial filaments, the apex of each of which is terminated by a strong sickle-shaped hook (fig. 6, IV). The majority of the branchial filaments of the stem are also terminated either by smaller hooks or by short straight spines. Long setæ, hooked at the ends, and otherwise similar in structure to those of *Astacopsis*, are attached to the posterior edge of the stem of the podobranchia (fig. 6, VII).

The ala is widest, and extends furthest towards the summit of the branchia, in the most anterior podobranchia, while in the hindermost it is reduced to little more than a longitudinal ridge. This branchia, in fact, is very similar to one of those of *Astacopsis*.

There are six anterior arthrobranchiæ, which are not more than half as long as the podobranchiæ, and five still smaller posterior arthrobranchiæ, the hindermost of which is almost rudimentary.

As in *Astacopsis*, there are four large pleurobranchiæ, the hindermost of which is only slightly larger than the other three, which are nearly equal in size.

Small branchial filaments are scattered over the whole posterior face of the epipodite of the first maxillipede; and the apex of each is provided with a strong sickle-shaped hook.

The coxopoditic setæ are relatively short, as in *Astacopsis*, but slender and curved, and even slightly undulating (fig. 6, VI). Each is hooked at its free extremity (fig. 6, V).

If the distinctive character of *Chæraps*, as given by Erichson, is correct, this is not a true *Chæraps*; but the branchiæ of these

[1] My best thanks are due to Dr. Günther, F.R.S., for the readiness with which he has aided my investigations by giving me free access to the Crustacean collection under his charge.

animals are so readily detached, that I can give no opinion on this point without comparison with the original specimens. In any case,

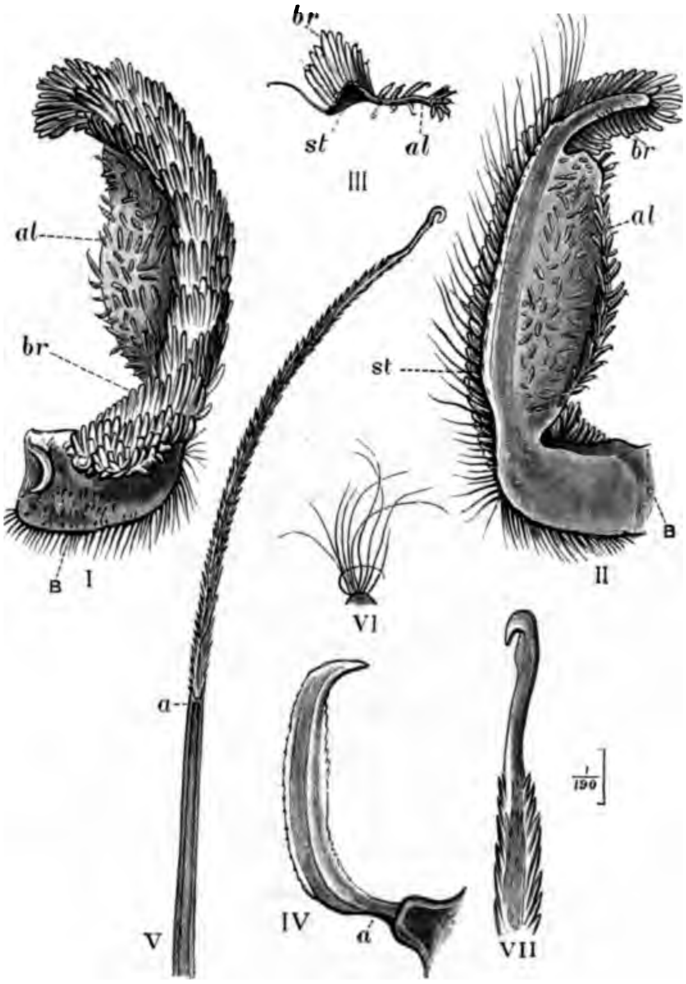

FIG. 6.—*Chæraps* (?).

I. The outer face of the podobranchia of the antepenultimate thoracic limb of the left side (× 3). II. The inner face of the same podobranchia: B, basal portion; *st*, stem; *al*, ala; *br*, branchial filaments. III. A transverse section of the middle of the podobranchia (× 3). IV. A sickle-shaped hook of a branchial filament $\frac{1}{100}$ of an inch in length. V. One of the coxopoditic setæ more highly magnified: *a*, the circumferential inflexion of the wall of the seta. The central canal does not stop at this point, but is continued to the end of the seta. VI. A bundle of coxopoditic setæ (× 3). VII. The extremity of one of the long setæ of the posterior edge of the stem. The vertical line represents $\frac{1}{100}$ of an inch magnified to the same extent.

the structure of the podobranchiæ shows the distinctness of this form from *Astacopsis*.

The Branchial formula of Chæraps (?).

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleuro-branchiæ.		
VII............	o (ep *r*)	o	o	o	=	o (ep *r*)
VIII............	1	1	o	o	=	2
IX............	1	1	1	o	=	3
X............	1	1	1	o	=	3
XI............	1	1	1	1	=	4
XII............	1	1	1	1	=	4
XIII............	1	1	1	1	=	4
XIV............	o	o	o	1	=	1
	6 + ep *r* + 6	+	5	+ 4	=	21 + ep *r*.

5. *The Branchiæ of* Engæus.

The number, the general disposition, and the structure of the branchiæ are the same as in *Astacopsis* and *Chæraps.*

The podobranchiæ have no vestige of a lamina. The first podobranchia has a small ala, much as in *Chæraps*; but only a few of the branchial filaments have terminal hooks.

The arthrobranchiæ are very small, those of the posterior series being the smaller; and the three anterior pleurobranchiæ are much smaller than the hindermost.

In all the branchiæ, and especially in the arthrobranchiæ and pleurobranchiæ, the terminal filament is exceptionally long and thick.

There are only a few very small hooked papillary elevations on the epipodite of the first maxillipede; in fact the podobranchia is reduced to nearly the same condition as in *Astacus.* The hooks of the setæ are very slender.

The branchial formula is the same as in *Astacopsis* and *Chæraps* viz :—

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleuro-branchiæ.		
VII............	o (ep *r*)	o	o	o	=	o (ep *r*)
VIII............	1	1	o	o	=	2
IX............	1	1	1	o	=	3
X............	1	1	1	o	=	3
XI............	1	1	1	1	=	4
XII............	1	1	1	1	=	4
XIII............	1	1	1	1	=	4
XIV............	o	o	o	1	=	1
	6 + ep *r* + 6	+	5	+ 4	=	21 + ep *r*

6. *The Branchiæ of* Paranephrops.

In *Paranephrops planifrons* I find the branchiæ to have the same general character and disposition as in *Astacopsis* and *Engæus*.

The podobranchiæ are devoid of any trace of a lamina. The branchial filaments on the posterior faces of these branchiæ are, for the most part, provided with terminal hooks, while the rest have smooth and rounded apices.

The anterior arthrobranchiæ have not half the size of the podobranchiæ, while the posterior arthrobranchiæ are very minute, and the hindermost is rudimentary, being a mere simple filament, like one of the rudimentary pleurobranchiæ of *Astacus*. The pleurobranchiæ are larger, but the three anterior ones are small. None of these branchiæ have hooked papillæ.

The external and posterior face of the epipodite of the first maxillipede is beset with short hooked branchial filaments.

The coxopoditic setæ are few, slender, short, and hooked at the extremity.

The Branchial formula of Paranephrops.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ.		Pleurobranchiæ.		
		Anterior.	Posterior.			
VII	0 (ep *r*)	0	0	0	=	0 (ep *r*)
VIII	1	1	0	0	=	2
IX	1	1	1	0	=	3
X	1	1	1	0	=	3
XI	1	1	1	1	=	4
XII	1	1	1	1	=	4
XIII	1	1	*r*	1	=	3 + *r*
XIV	0	0	0	1	=	1
	6 + ep *r*	+ 6 +	4 + *r*	+ 4	=	20 + ep *r* + *r*.

The branchiæ of two specimens of a *Paranephrops*, from the Fiji Islands, like the foregoing in the British Museum, are in such bad condition, the specimens having apparently got dry before they were placed in spirits, that I cannot make out all the details of their structure; but, so far as it can be ascertained, they agree with those of the preceding species.

7. *The Branchiæ of* Parastacus.

By the kindness of Prof. Peters, I have been able to examine two well preserved males of the *Astacus brasiliensis* and *A. pilimanus* of Von Martens; and the results are very interesting.

The branchiæ of the two species are so much alike that they may be described together. In many points they resemble those of

Chæraps; but the structure is by no means identical; and as these Crayfishes are peculiar in other respects, I think it will be most convenient to consider them as members of a distinct genus, *Parastacus*.

There are six ordinary podobranchiæ, of which, as usual, the first is the smallest, the next two are longer, and the last three are longest of all and nearly equal. In the podobranchia of the second maxillipede, the inner lip of the groove of the stem of the branchia is produced into a broad ala, as in *Chæraps*; but the ala becomes broader towards the apex, and is there abruptly truncated. The truncated edge is fringed by a single series of branchial papillæ. The posterior lip of the groove is beset with long hooked setæ. In the four following podobranchiæ the ala is a little narrower, especially at its apex, but it has essentially the same characters. In the last the ala is present in the basal half of the stem, but narrows to a mere ridge in the apical half.

The modified podobranchia of the first maxillipede bears from ten to sixteen longer or shorter branchial filaments on the outer half of the posterior surface of its apical end (fig. 2, D, p. 759).

The six anterior arthrobranchiæ are full-sized, and increase in length from before backwards. The five posterior arthrobranchiæ are much smaller; and the last is rudimentary, consisting of a very short slender stem, with from one to three lateral filaments.

There are four pleurobranchiæ, all well developed, but the hindermost the longest.

In the podobranchiæ, many of the posterior branchial filaments are terminated by hooks. As usual, these are absent in the other branchiæ.

The coxopoditic tubercles give origin to bundles of long and tortuous setæ, with hooked apices. These are neither so long nor so numerous, as in *Astacus* and *Cambarus*, but are more like them than are those of any other *Parastacidæ*.

The Branchial formula of Parastacus.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII............	o (ep *r*)	o	o	o	=	o (ep *r*)
VIII............	1	1	o	o	=	2
IX............	1	1	1	o	=	3
X............	1	1	1	o	=	3
XI............	1	1	1	1	=	4
XII............	1	1	1	1	=	4
XIII............	1	1	*r*	1	=	3 + *r*
XIV............	o	o	o	1	=	1
	6 + ep *r* +	6 +	4 + *r* +	4	=	20 + ep *r* + *r*.

8. *The Branchiæ of* Astacoides.

I am indebted to the courtesy of Prof. Alphonse Milne-Edwards for the opportunity of examining the branchiæ of a male specimen of the Crayfish of Madagascar, *Astacoides madagascariensis.* On account of the rarity of this species, it is desirable to describe its branchial apparatus in some detail. The length of the specimen was 5·7 inches.

The branchiostegite of the left side being carefully removed, the six large podobranchiæ were seen. The first, 0·9 inch long (measured from its attachment to its apex), was directed upwards and backwards in the cervical depression. The second, 1 inch long, took a similar direction, but was concave forwards. The third, slightly shorter, lay parallel with the second. The fourth (fig. 7, I, II) was much longer; bent round the third, its summit touched the apex of the second; the total length of the branchia when straightened out was about 1·3 inch. The fifth branchia was still longer, curving round the posterior edge of the last, so that its apex touched the front boundary of the branchial cavity. The sixth branchia started from a higher level than any of the others, in consequence of the great size of the coxopodite of the penultimate thoracic limb; its length was 1·05 inch; and it was nearly straight, its apex fitting into the summit of the branchial cavity. The base of each podobranchia is elongated upwards, as in *Astacopsis*; and there is a soft fold of integument over its attachment. There is no trace of any lamina.

On the removal of the podobranchiæ the arthrobranchiæ came into view. But, in contradistinction to all other known Crayfishes, there are only five of them fully developed, and even these are remarkably small in comparison with the podobranchiæ. The first is the shortest (0·5 in.); and they increase in length to the hindermost, which is 0·35 in. long. Each is concave forwards and convex backwards; and the apex of the hindermost comes within 0·15 inch of the nearest part of the anterior superior boundary of the branchial cavity. In all these branchiæ the branchial filaments are very numerous, stiff, relatively short and close set; so that they approach the characters of the branchiæ of the Lobster. The groove on the inner face of the stem seems, at first, to be reduced to nothing in the upper part of the podobranchiæ. However, a transverse section (fig. 7, III) shows that it exists and is bounded by two lips, the anterior of which is produced into a narrow ala. But the numerous hooked branchial filaments, which arise from the posterior face of the stem, fill the groove and appear to obliterate it.

The hindermost of the arthrobranchiæ is attached close to the articulation of the coxopodite with the epimeron, and is therefore in the same position as one of the anterior series of arthrobranchiæ in other Crayfishes. There is not the slightest trace of the attach-

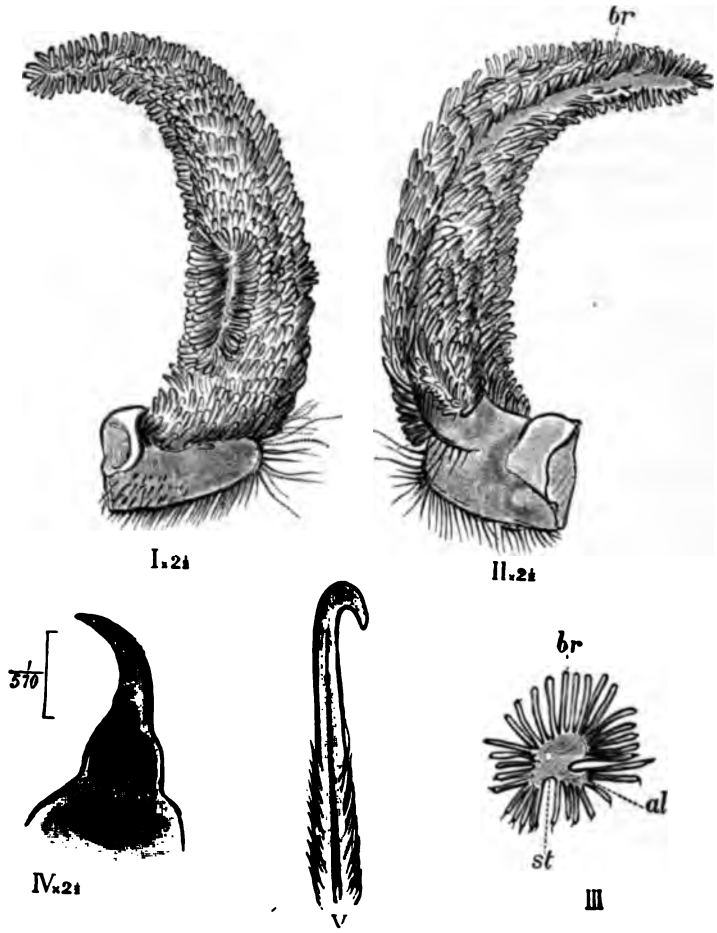

FIG. 7.—*Astacoides madagascariensis.*

I The outer face of the podobranchia of the antepenultimate thoracic limb of the left side (× 2½). II. The inner face of the same: *br*, branchial filaments. III. A transverse section of the middle of the podobranchia: *st*, the grooved inner face of the stem. IV. The terminal hook of a branchial filament; and V. The apex of a coxopoditic seta. The straight line represents $\frac{1}{510}$? of an inch magnified to the same extent as these.

ment of another branchia on the arthrodial membrane behind this. But on the epimeron, just above the margin of the articular cavity, and 0·1 inch behind the root of the anterior branchia, a minute

filament, 0·05 in. long, which I take to be a rudiment of the posterior branchia, enclosed by the downward extension of the epimeron, projects.

The attachment of the next arthrobranchia is like that of its predecessor, but not quite so far forward. At a distance of 0·5 in. behind and above its root, an exceedingly minute papilla, not more than a fifth of the length of the foregoing, is enclosed in the articular edge of the epimeron. This is doubtless the rudiment of the posterior arthrobranchia. The three remaining arthrobranchiæ are fixed into the arthrodial membranes of the other ambulatory and prehensile limbs, in a position corresponding with that occupied by the fourth. In the case of the hindermost of these, or that of the eleventh pair of appendages, there is, above and behind the root of the gill, and 0·08 inch distant from it, a filamentous, rudimentary branchia rather less than 0·1 inch long attached within the articular margin of the epimeron. Three or four minute unequal processes are given off from the posterior edge of this filament. There is another very small papillary rudiment immediately above and behind the root of the next arthrobranchia ; but none could be discovered above that of the most anterior arthrobranchia.

In addition to the five conspicuous and functional outer arthrobranchiæ, there was another very small one, only 0·18 inch long, and almost rudimentary, attached to the second maxillipede.

The pleurobranchia of the last thoracic somite was only 0·3 inch long, and was hardly visible at first, from being overlapped by the hindermost podobranchia. I could not discover the slightest trace of any other pleurobranchiæ.

The upper part of the modified podobranchia of the first maxillipede is sharply folded upon itself longitudinally; and its outer lobe is beset with numerous short branchial filaments, most of which have terminal hooks. Similar hooked filaments are to be found about the base and the posterior region of the other podobranchiæ; but a large proportion of the filaments of these branchiæ, and all of those of the arthrobranchiæ, appear to be hookless.

The tubercles of the coxopodites give rise to small tufts of short and straight setæ, which are hooked at the end, like those of *Astacopsis* (fig. 7, v). The hinder and upper setæ of the bases of the podobranchiæ are similarly hooked ; but, as in the other species, the anterior setæ are straight, or only slightly curved at the extremities.

The Branchial formula of Astacoides madagascariensis.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.			
VII...........	o (ep *r*)	o	o	o	=	(ep *r*)	
VIII...........	1	*r*	o	o	=	1 +	*r*
IX...........	1	1	o	o	=	2	
X...........	1	1	*r*	o	=	2 +	*r*
XI...........	1	1	*r*	o	=	2 +	*r*
XII...........	1	1	*r*	o	=	2 +	*r*
XIII...........	1	1	*r*	o	=	2 +	*r*
XIV...........	o	o	o	1	=	1	
	6 + ep *r*	+ 5 + *r*	+ 4 *r*	+ 1	=	12 + ep *r* + 5 *r*.	

In *Astacoides*, therefore, the branchiæ have suffered more reduction than in any other known Crayfish; and this reduction is, as it were, a continuation of the process already commenced in *Engæus* and *Paranephrops*, in which the anterior pleurobranchiæ and the posterior arthrobranchiæ are small, or even rudimentary.

III. The Classification of the Crayfishes.

Whatever may be the variation in the structure of the branchiæ of the different species of Crayfish, it will be observed that they all agree in possessing podobranchiæ, or branchiæ attached to the coxopodites, of the six middle thoracic appendages, and that these are either not at all, or incompletely, differentiated into a branchial and an epipoditic division. Moreover, *Astacopsis*, *Chæraps*, *Engæus*, *Paranephrops*, *Parastacus*, and *Astacoides*, in which the apices of the podobranchiæ are not separated into a branchial plume and a well developed lamina, present a less differentiated type of branchial structure than that which obtains in *Astacus* and *Cambarus*.

Thus the structure of the branchiæ in the Crayfishes separates them into two groups, of which I propose to term the latter the Potamobiidæ, and the former the Parastacidæ.

In the Parastacidæ the podobranchiæ are devoid of more than a rudiment of a lamina, though the stem may be alate. The podobranchia of the first maxillipede has the form of an epipodite; but, in almost all cases, it bears a certain number of well-developed branchial filaments.

The first abdominal somite possesses no appendage in either sex; and the appendages of the four following somites are large.

The telson is never completely divided by a transverse suture.

More or fewer of the branchial filaments of the podobranchiæ are terminated by short hooked spines; and the coxopoditic setæ, as well as those which beset the stems of the podobranchiæ, have hooked apices.

In the POTAMOBIIDÆ the podobranchiæ of the second, third, fourth, fifth, and sixth thoracic appendages are always provided with a large plaited lamina. The podobranchia of the first maxillipede is converted into an epipodite, entirely devoid of branchial filaments.

The first abdominal somite invariably bears appendages in the male, and usually in both sexes. In the male these appendages are styliform, and those of the second somite are always peculiarly modified.

The appendages of the four following somites are relatively small.

The telson is usually completely divided by a transverse suture.

None of the branchial filaments are terminated by hooks; nor are any of the coxopoditic setæ or the longer setæ of the podobranchiæ hooked, though hooked tubercles occur on the stem and on the lamina of the latter.

The coxopoditic setæ are always long and tortuous.

It is worthy of notice that the Parastacidæ agree with the Palinuridæ and Scyllaridæ in the abortion of the appendages of the first abdominal somite, and in possessing hooked setæ, while in the Potamobiidæ, as in the Lobsters, the setæ are not hooked, and, as in almost all the Podophthalmia, except the Palinuridæ and Scyllaridæ,[1] the appendages of the first abdominal somite are present, and are specially modified in the males.

Of the six genera of the Parastacidæ, *Astacoides* is widely separated from all the rest by the reduction of the number of its functional branchiæ to twelve, while all the other genera at present known have, at fewest, twenty, and usually twenty-one, branchiæ.

Astacopsis, *Chæraps*, *Engæus*, and *Parastacus* have, in common, a long epistoma, the surface of which is flattened, the basal joint of the antennæ fixed by the overlapping edge of the cephalostegite, the posterior thoracic sterna narrow, the coxopodites of the hinder thoracic limbs large and approximated in the middle line. The rostrum and the antennary squame are short. *Engæus* is distinguished among these, not only by the narrowness of the first abdominal somite, but by the form of the anterior part of the head, with its short and deflexed rostrum, and very small antennary squame.

In *Chæraps* the podobranchiæ are alate, in *Astacopsis* they are

[1] In *Gebia*, *Calliaxis*, and *Porcellana*, the first abdominal appendages are rudimentary or abortive in the male sex.

not. *Parastacus* somewhat resembles *Chæraps* in its alate podobranchiæ, but differs from all the rest by possessing long and tortuous coxopoditic setæ.

I have nothing to add to the distinctive characters of the two genera of the Potamobiidæ, *Astacus* and *Cambarus*, already given by Erichson, Hagen, and others.

All the branchiæ of the Crayfishes consist of a stem beset with numerous cylindrical filaments. In fact, they are typical examples of what are termed by Milne-Edwards "branchies en brosse," and may be called "trichobranchiæ," in contradistinction to the lamellar gills or "phyllobranchiæ," which are met with in a large number of other Crustacea. The whole of the Macrurous Podophthalmia, excepting the genera *Gebia* and *Callianassa*, the Prawns, the Shrimps, and the Mysidæ, have trichobranchiæ.

In the Mysidæ the branchiæ are rudimentary or absent, and in the Euphausidæ and Penæidæ they are peculiarly modified. In the Prawns and Shrimps, in *Gebia* and *Callianassa*, in all the Anomura and Brachyura, the gills are phyllobranchiæ.

Thus the Podophthalmia or Thoracostraca (to use the convenient name proposed by Prof. Claus) are divisible in respect of the structure of their respiratory organs into three groups, which may be termed Abranchiata, Trichobranchiata, and Phyllobranchiata.

Among the trichobranchiate Podophthalmia, the Euphausidæ possess no other than podobranchiæ.[1] These are mere respiratory plumes presenting no differentiation even into base and stem. All the rest of the Trichobranchiata have arthrobranchiæ, either with or without functional podobranchiæ and pleurobranchiæ. Among those which possess all three kinds of branchiæ, the Parastacidæ and the Palinuridæ are highly exceptional among the Thoracostraca in the absence of the appendages of the first abdominal somite in both sexes. They further, as a rule, possess 21 branchiæ (*pdb.* 6, *arb.* 11, *plb.* 4), though the number is, in some cases, reduced by the suppression of more or fewer of the arthrobranchiæ, and pleurobranchiæ.

In most, if not all the other Trichobranchiata, the first abdominal appendages of the males are present and specially modified. Among these, the Potamobiidæ are characterised by the imperfect division of their podobranchiæ into a proper branchial and an epipoditic portion.

[1] Possibly some of the branchial plumes in *Sergestes* may be attached to the arthrodial membranes. A critical examination of the species of *Sergestes* in reference to this point would probably yield interesting results.

In *Homarus* and *Nephrops*, *Axius* and *Thalassina*, the podobranchiæ are completely differentiated, from their bases onward, into a proper branchial and an epipoditic portion. In this condition the podobranchia is usually described as an epipodite, to the base of which a branchia is attached.

In *Homarus* the branchial filaments are numerous and multiserial, and the branchial formula is:—

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII	0 (ep)	0	0	0	=	0 (ep)
VIII	1	0	0	0	=	1
IX	1	1	1	0	=	3
X	1	1	1	0	=	3
XI	1	1	1	1	=	4
XII	1	1	1	1	=	4
XIII	1	1	1	1	=	4
XIV	0	0	0	1	=	1
	6 + ep +	5 +	5 +	4	=	20 + ep.

In *Nephrops* the branchiæ have the same structure, but the branchial plume of the podobranchia of the second maxillipede is absent or rudimentary; hence the number of the branchiæ is reduced to 19.

In *Axius* the podobranchia of the penultimate thoracic limb is reduced to an epipodite by the disappearance of the branchial plume, and the hindermost pleurobranchia is also wanting. The arthrobranchia of the second maxillipede is represented by a mere rudiment.

The Branchial formula of Axius stirhynchus.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII	0 (ep)	0	0	0	=	0 (ep)
VIII	1	*r*	0	0	=	1 + *r*
IX	1	1	1	0	=	3
X	1	1	1	0	=	3
XI	1	1	1	1	=	4
XII	1	1	1	1	=	4
XIII	0 (ep)	1	1	1	=	3 + ep
XIV	0	0	0	0	=	0
	5 + 2 ep +	5 + *r* +	5 +	3	=	18 + 2 ep + *r*.

The branchial filaments in this genus, again, are arranged only in two series on the stem, though, as they remain filiform, the approximation to the phyllobranchiate type is but slight.

In *Homarus*, *Nephrops*, and *Axius* the epipoditic divisions of the podobranchiæ are very large; but in *Thalassina*, *Stenopus*, and *Penæus* they are much reduced in size, and the branchial element disappears in more than the hindermost.

In *Thalassina scorpioides* the last thoracic somite is provided with no branchiæ of any kind, nor have its limbs any epipodite, and there are no pleurobranchiæ. The podobranchiæ of the twelfth and thirteenth somites are reduced to stout curved setose epipodites. In the eleventh there is a similar epipodite, but a branchial plume springs from its base. The tenth had a small epipodite, without a branchia in the specimen examined; but I am inclined to think that the branchia may have become detached; for the similar epipodite of the external maxillipede bore a mutilated, or rudimentary, small branchia. The small epipodites of the second maxillipedes figured by Milne-Edwards were broken off; but the places to which they were attached were discernible. The first maxillipede had no epipodite, in which respect *Thalassina* approaches *Callianassa.*

There are twelve arthrobranchiæ attached in pairs, from the second maxillipede to the penultimate thoracic limb inclusively. All these branchiæ are remarkable from the fact that, for a greater or less distance from the base of the gill, the stem is provided with broad imbricated foliaceous expansions, which are traversed by ramified vessels, and take the place of the branchial filaments, which are sometimes very few, and confined altogether to the basal region of the branchia. These branchial plates differ from those of the true phyllobranchiæ in their small number and in their disposition, inasmuch as they are directed obliquely to the stem and not at right angles to it. Nevertheless it is interesting to find, in both *Axius* and *Thalassina*, a certain approach to the phyllobranchiate type, which is completely reached in *Gebia* and *Callianassa.*

The Branchial formula of Thalassina.

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ.		Pleuro-branchiæ.		
		Anterior.	Posterior.			
VII...........	0	0	0	0	=	0
VIII...........	0 (ep)	1	1	0	=	2 + ep
IX...........	1	1	1	0	=	3
X...........	1	1	1	0	=	3
XI...........	1	1	1	0	=	3
XII...........	0 (ep)	1	1	0	=	2 + ep
XIII...........	0 (ep)	1	1	0	=	2 + ep
XIV...........	0	0	0	0	=	0
	3 + 3 ep +	6 +	6 +	0	=	15 + 3 ep.

In *Stenopus hispidus* the branchiæ resemble those of *Astacopsis* in structure, the filaments being loose, slender, and multiserial. But the disappearance of the branchial plumes from the podobranchiæ has gone still further than in *Thalassina*; and all these organs are reduced to delicate, almost vesicular epipodites entirely devoid of any proper branchial filaments, except in the case of the second maxillipede, in which a few such filaments are attached to the base of the epipodite. Moreover the number of the pleurobranchiæ is increased to seven.

The Branchial formula of Stenopus.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII.........	o (ep)	?	o	o	=	(ep)
VIII.........	o (ep *r*)	1	1	1	=	3 + ep
IX.........	o (ep)	1	1	1	=	3 + ep
X.........	o (ep)	1	1	1	=	3 + ep
XI.........	o (ep)	1	1	1	=	3 + ep
XII.........	o (ep)	1	1	1	=	3 + ep
XIII.........	o (ep)	1	1	1	=	3 + ep
XIV.........	o	o	o	1	=	1
	o + 7 ep + *r* + 6	+ 6		+ 7	=	19 + 7 ep + *r*.

I am inclined to suspect the existence of a rudimentary anterior arthrobranchia in VII.; but I could not make sure of it.

By the structure of its branchiæ *Stenopus* is sharply separated from *Penæus*, with which it has hitherto been associated, although it approaches *Penæus* in the almost complete abortion of the branchial element of the podobranchiæ. In the Penæidæ, in fact, each branchia consists of a stem which is pointed at both ends and gives off two series of opposite lateral branches. This stem is attached by a pedicle near its lower end. Near each end of the stem the lateral branches are very short, and stand straight out; but they rapidly become longer; and as they do so they curve outwards towards one another, and eventually meet in the middle line. The middle of the branchia consequently assumes the form of a hollow cylinder.

The outer face of each lateral branch gives off a close-set series of secondary branches, which diminish in size towards the free end of the lateral branch, and at the free end are simple undivided filaments. But towards the attached end of the branch the secondary branches are themselves dichotomously subdivided in the

direction of their length; so that the most complicated of these secondary branches presents a short stem whence two branches proceed, each of these again gives off two, and these may terminate in yet other two. Hence each secondary branch is like a flat triangular plate slit by fissures of varying depths, and attached by its apex to a lateral branch. All these secondary branches are directed upwards and outwards.

A detached lateral branch closely resembles one of the branchiæ of *Thysanopoda*; while, so far as I can judge from the figures given by Kröyer[1] and Sars,[2] the branchiæ of *Sergestes* and *Lophogaster* still more closely approach those of *Penæus*.

A similar structure was described by Duvernoy in *Aristæus*, and was supposed by him to be characteristic of that genus; but Dana has already justly expressed a doubt whether, in this respect, *Aristæus* differs from the other Penæidæ.

In *Penæus*, the last and the penultimate thoracic limbs present no trace of podobranchiæ; and in all the rest the podobranchia is reduced to a small epipodite, which, in the middle of the series, is bifurcated at its free end. The latter lies between the arthrobranchiæ of its own somite and the next following. There are seven pleurobranchiæ, of which the hindermost is the largest, while the most anterior is very small.

The Branchial formula of Penæus brasiliensis.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII	o (ep)	1 (small)	o	o	=	1 + ep
VIII	o (ep)	1	1	1	=	3 + ep
IX	o (ep)	1	1	1	=	3 + ep
X	o (ep)	1	1	1	=	3 + ep
XI	o (ep)	1	1	1	=	3 + ep
XII	c (ep)	1	1	1	=	3 + ep
XIII	o	1	1	1	=	3
XIV	o	o	o	1	=	1
	o + 6 ep +	7 +	6 +	7	=	20 + 6 ep.

The arthrobranchia of VII. is very small; in fact, it is a mere tuft of dichotomously divided branchial filaments.

The results of this examination of the principal forms of those

[1] Forsög til en monographisk Fremstilling af Kraebsdyrslagten *Sergestes*: 1855.
[2] Beskrivelse over *Lophogaster typicus*: 1862.

Trichobranchiata which possess more than one kind of branchiæ may be thrown into a tabular form, as follows :—

I. No appendages to the first abdominal somite in either sex. *Astyla.*
- 1. Podobranchiæ undivided .... PARASTACIDÆ.
- 2. Podobranchiæ divided into branchial and epipoditic portions ...... PALINURIDÆ.

II. Appendages of the first abdominal somite almost always present, and specially modified in the males. *Stylophora.*
- 1. Podobranchiæ partially divided .... POTAMOBIIDÆ.
- 2. Podobranchiæ completely divided or reduced to epipodites.
  - *a.* Pleurobranchiæ not more than four.
    - *α.* Posterior pleurobranchia present, and the most posterior of the podobranchiæ complete .... HOMARIDÆ. *Homarus*, *Nephrops.*
    - *β.* Posterior pleurobranchia wanting, and more or fewer of the posterior podobranchiæ reduced to epipodites.
      - *a.* Branchiæ with only filamentous processes .... *Axius.*
      - *b.* Branchiæ with foliaceous as well as filamentous processes .... *Thalassina.*
  - *b.* Pleurobranchiæ more than four.
    - *α.* Branchiæ filamentous .... *Stenopus.*
    - *β.* Branchiæ ramose .... *Penæus.*

All the Trichobranchiata are Macrura, in the sense of having the abdomen and its appendages well developed ; but, in *Ibacus* and *Thenus*, the abdomen becomes shortened and the cephalothorax wide, while the antennary and the ocular regions are modified in a manner very similar to that which gives rise to the peculiar " face " or " metope " of the typical Brachyura. A very little further modification would convert *Thenus*, for example, into a tricho-branchiate Crab. Such forms as these, which simulate the Brachyura, and yet differ profoundly from them, may be termed " pseudo-carcinoids."

If the branchial filaments of *Axius* were shortened and widened, the structure of the branchiæ would approach that which obtains in *Gebia* and *Callianassa*, which are truly phyllobranchiate. But in other respects there is a wide interval between these genera, on the one hand, and *Axius* and *Thalassina*, which are ordinarily associated with them among the Thalassinidæ, on the other hand ; for the podobranchiæ have entirely disappeared on the six hinder thoracic limbs, and even on the first or second maxillipede they are represented only by rudimentary epipodites.

There are no pleurobranchiæ ; and the total number of gills is reduced to five pairs of arthrobranchiæ on each side.

The Branchial formula of Gebia *and* Callianassa.

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleuro-branchiæ.		
VII	o	o	o	o	=	o
VIII	o	o	o	o	=	o
IX	o	1	1	o	=	2
X	o	1	1	o	=	2
XI	o	1	1	o	=	2
XII	o	1	1	o	=	2
XIII	o	1	1	o	=	2
XIV	o	o	o	o	=	o
	o +	5 +	5 +	o	=	10

In the almost complete abortion of the podobranchiæ, and in the presence of ten arthrobranchiæ attached in pairs to the middle thoracic somites, *Gebia* and *Callianassa* agree with *Porcellana*, *Galathea*, *Lithodes*, *Pagurus*, and *Remipes*. But in *Galathea* and *Porcellana* the four hindermost pleurobranchiæ are present, making fourteen gills on each side ; in *Lithodes* and *Pagurus* the penultimate pleurobranchia exists, making eleven ; in *Remipes* there is no pleurobranchia, and only nine arthrobranchiæ, viz. one on the ninth and two for each of the four following somites, are present.

In this group, which nearly corresponds with the Anomala of De Haan, and which I propose to term the "Anomomorpha," there is every degree of modification—from such typically Macrurous forms as *Gebia* and *Galathea* to such pseudo-carcinoids as *Lithodes* and *Porcellana*. It is interesting to remark, however, that, while in *Thenus* and *Ibacus* the process of modification has chiefly affected the head, in the Anomomorpha the characteristic changes are more marked in the abdomen. In none of the latter are the basal joints of the antennæ fixed, nor are distinct orbits formed.

It is easy to understand the possibility of the derivation of the Anomomorpha from some form allied to *Axius* and *Thalassina* (but with four pleurobranchiæ) by the further reduction, and final almost complete disappearance, of the podobranchiæ, while the biserial filaments of the other gills flattened out and became lamellar.

The Prawns and Shrimps ("Salicoques" of Milne-Edwards, *Carides* of De Haan), if we exclude the Penæidæ, constitute a natural assemblage, to which I will apply the name of "Caridomorpha." They are all eminently Macrurous ; and the characteristic feature of their branchial system is the predominance of the pleurobranchiæ, and the concomitant diminution in the number and the importance of

the arthrobranchiæ and of the podobranchiæ. In fact, so far as I am aware, there are never any traces of the latter except upon the maxillipedes.

In both *Palæmon* and *Crangon* I find five pleurobranchiæ attached to the posterior thoracic somites, from the tenth to the fourteenth inclusively. In *Palæmon*, two arthrobranchiæ, one of which is very small, are attached to the arthrodial membrane of the external maxillipede, which has a very short and rudimentary epipodite. The second maxillipede bears a podobranchia divided into a small branchia and an oval epipoditic plate. In the first maxillipede the place of the podobranchia is occupied by a rounded bilobed lamella.

In *Crangon* none of the maxillipedes bear gills. The epipodite of the first maxillipede is relatively much larger and triangular; that of the second is tongue-shaped and almost vesicular; that of the third is a mere rounded process.

I can find only one arthrobranchia on the ninth somite.

The Branchial formula of Palæmon.

Somites and their appendages.	Podo-branchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleuro-branchiæ.		
VII	0 (ep)	0	0	0	=	0 (ep)
VIII	1	0	0	0	=	1
IX	0 (ep)	1	1	0	=	2 + ep
X	0	0	0	1	=	1
XI	0	0	0	1	=	1
XII	0	0	0	1	=	1
XIII	0	0	0	1	=	1
XIV	0	0	0	1	=	1
	1 + 2 ep +	1 +	1 +	5	=	8 + 2 ep.

From the number of their pleurobranchiæ the Caridomorpha cannot be regarded as a reduced modification of any of the Trichobranchiata, except the Penæidæ and *Stenopus*. But it is easy to derive them from a *Stenopus*-like primitive form by the reduction of the podobranchiæ and the arthrobranchiæ, and the conversion of the five posterior pleurobranchiæ into gills of the lamellar type.

In the Brachyura of Milne-Edwards the disposition of the branchial apparatus is well known to be definite and characteristic. In *Cancer pagurus*, for example, there are nine branchiæ; seven of

these are pyramidal in form, and take a general direction from the base towards the apex of the branchial chamber, to the inner walls of which they are applied. The two posterior of these gills are pleurobranchiæ, being attached respectively to the epimera of the eleventh and the twelfth somites. The fifth and fourth, the third and second, are fixed in pairs by a common pedicle to the arthrodial membrane of the appendages of the tenth and ninth somites—that is, the great forceps and the third maxillipede. The most anterior gill, slenderer than the others, is attached to the arthrodial membrane of the second maxillipede. There are therefore five arthrobranchiæ.

The podobranchia of the first maxillipede is represented only by the large curved epipodite, which sweeps over the surface of the arthrobranchiæ and the pleurobranchiæ. The podobranchia of the second maxillipede is divided into a branchial plume, which lies horizontally under the bases of the four anterior arthrobranchiæ, and an epipodite, which ascends between the arthrobranchia of its somite and those of the next, and lies internal to the latter, close to the inner wall of the branchial cavity.

In the third maxillipede the epipodite is very long, and forms the valve to the afferent aperture of the branchial cavity. Attached to its base is a short truncated branchia, which fits in between the bases of the second and the third arthrobranchiæ.

The Branchial formula of Cancer pagurus.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII.........	o (ep)	o	o	o	=	o (ep)
VIII.........	1	1	o	o	=	2
IX.........	1	1	1	o	=	3
X.........	o	1	1	o	=	2
XI.........	o	o	o	1	=	1
XII.........	o	o	o	1	=	1
XIII.........	o	o	o	o	=	o
XIV.........	o	o	o	o	=	o
	2 + ep +	3 +	2 +	2	=	9 + ep.

A considerable reduction of the branchial apparatus occurs in some Brachyura, especially the *Catometopa*. Thus, in *Gelasimus* the hinder pleurobranchia and the most anterior arthrobranchia have disappeared, and the two podobranchiæ are so small as to be almost rudimentary.

In the Raninidæ and in *Latreillia*, the Brachyurous metope is incompletely formed; but the branchial system is essentially that of the true Crabs. The same may be said of *Dromia*, although the branchial apparatus of this crustacean presents some very interesting approximations to the less-modified type from which it cannot be reasonably doubted that the Brachyura have proceeded.

The epipodites of the three maxillipedes are very similar in form and disposition to those of the ordinary Crabs; and that of the second bears a small horizontal branchial plume. That of the third sometimes bears a small branchia. The coxopodite of the fourth thoracic limb has a small epipodite; but I find no trace of such an appendage on the rest of the thoracic limbs. Moreover there are five pairs of arthrobranchiæ attached to consecutive somites from the ninth to the thirteenth—and four pleurobranchiæ, one for each of the four posterior thoracic somites.

The Branchial formula of Dromia.

Somites and their appendages.	Podobranchiæ.	Arthrobranchiæ. Anterior.	Arthrobranchiæ. Posterior.	Pleurobranchiæ.		
VII...........	o (ep)	o	o	o	=	o (ep)
VIII...........	1	o	o	o	=	1
IX...........	1	1	1	o	=	3
X...........	o	1	1	o	=	2
XI...........	o	1	1	1	=	3
XII...........	o	1	1	1	=	3
XIII...........	o	1	1	1	=	3
XIV...........	o	o	o	1	=	1
	2 + ep +	5 +	5 +	4	=	16 + ep.

On comparing this branchial formula with that of *Homarus*, the relation between the two is obvious. In fact, if the three posterior podobranchiæ of the Lobster are suppressed, and the next is reduced to an epipodite, the branchial formula becomes the same as that of *Dromia*, and the remaining differences between the respiratory organs of the two result from the modification in form and structure of the branchial elements which remain. Thus it is a permissible, if not a probable, suggestion that, just as the Anomomorpha may have been derived from the modification of some form allied to *Axius*, and the Caridomorpha from some form allied to *Stenopus* and *Penæus*, so the Carcinomorpha (= the Brachyura and the Raninidæ, with *Homola* and *Dromia*) may have proceeded from some Homarine stock.

However this may be, the actual morphological relations of the

Thoracostraca appear to me to be represented with tolerable accuracy by the following scheme :—

CRUSTACEA.

THORACOSTRACA OR PODOPHTHALMIA.

III. PHYLLOBRANCHIATA.

CARIDOMORPHA. ANOMOMORPHA. CARCINOMORPHA.

II. TRICHOBRANCHIATA.

Palinuridæ.

$\underbrace{\textit{Penæidæ.}\quad\textit{Stenopidæ}}$ $\underbrace{\textit{Thalassinidæ.}\quad\textit{Axiidæ.}}$ $\underbrace{\textit{Homaridæ.}\quad\textit{Potamobiidæ.}}$ *Parastacidæ.*

Euphausidæ.

I. ABRANCHIATA.

Mysidæ.

STYLOPHORA. ASTYLA.

IV. The Distribution of the Crayfishes considered in relation to their Morphological Differences.

From what has been said above, it will be obvious that there is a remarkable correspondence between the morphological and the geographical divisions of the Crayfishes. Thus, all the Crayfishes of the northern hemisphere are Potamobiidæ, and all those of the southern hemisphere are Parastacidæ. In the northern hemisphere, again, the *Astaci* are Eurasiatic and West American, while the *Cambari* are characteristic of the North American region east of the Sierra Nevada—in other words, of the river-basins which flow into the Gulf of Mexico and the West Atlantic.

The *Astacine* region nearly answers to the Palæarctic province of Mr. Sclater, minus the southern shores of the Mediterranean, and plus Western North America; while the *Cambarine* region takes in most of the Palæarctic region, with the Neotropical region as far as Guatemala and the West Indies.

In the southern hemisphere, *Astacopsis*, *Chæraps*, and *Engæus* are confined to the Australian region, *Paranephrops* to New Zealand and the Fijis; while the South-American *Parastacus* is distinct from either of these, though closely allied with the Australian forms; and the peculiarity of the Madagascar fauna is vindicated by *Astacoides.*

Thus, if we were to establish provinces of distribution on the

Crayfishes alone, they would bear only a partial resemblance to those based on the association of terrestrial animals. On the other hand, if we compare the distribution of the Crayfishes with that of the freshwater fishes, there are, as might be expected, some curious points of resemblance. The distribution of the Salmonidæ, for example, corresponds pretty closely with that of the Potamobiidæ, though the range of the Salmonidæ extends less far to the south in North America, and a little further, namely, as far as Algeria in the Old World. Again, the Salmonidæ to the east of the Rocky Mountains are, for the most part, distinct from those to the west, while the genus *Onchorhynchus* is, like *Astacus*, common to both the Asiatic and the American shores of the North Pacific.

With the singular exception of *Retropinna*, there is no true Salmonoid in the southern hemisphere; but, as Dr. Günther has pointed out, the Haplochitonidæ and the Galaxiadæ, which stand in somewhat the same relation to the Salmonidæ as the Parastacidæ do to the Potamobiidæ, represent the Salmonidæ in the fresh waters of New Zealand, Australia, and South America.

It is worthy of remark that the Salmonidæ, the Haplochitonidæ, and the Galaxiadæ are singular among Teleostan fishes for the embryonic character of their female reproductive organs, which have no oviducts—just as, among the Podophthalmous Crustacea, the Crayfishes are distinguished by the undifferentiated character of their podobranchiæ.

With the exception of one or two species in Algeria and Asia Minor, the Salmonoids and their allies are wanting in the whole of Africa and Asia south of the great Asiatic highlands, just as the Crayfishes are. It will be very interesting to learn, from the thorough investigation of the fauna of Madagascar, which is now being carried out, whether the Salmonoids or their allies are in any way represented there.

The broad similarity in distribution between the Salmoniform fishes and the Crayfishes is doubtless due to the likeness of the conditions under which the two groups have reached their present development. I do not think that there can be any reasonable ground for questioning the assumption, that both the freshwater fishes and the freshwater Crustacea are modifications of a marine prototype, which has more or less completely adapted itself to freshwater conditions. In the case of the Crayfishes, at any rate, there is abundant analogical evidence in support of this hypothesis. It is well known that, in many parts of the world, the Prawns ascend rivers, and become fluviatile. The *Palæmon lacustris* (*Anchistia*

migratoria, Heller) of the Lago di Garda is identical with a Prawn now living in the Mediterranean. Again, the *Mysis relicta* of the lakes of Norway, Sweden, Western Russia, and North America (Michigan and Superior) is only a variety of the *Mysis oculata* of the Arctic seas.[1] Nor do I think it can be seriously questioned that the fluviatile and the land Crabs are modified descendants of marine Brachyura.

Let it be supposed that, at some former period of the earth's history, a Crustacean, similar to *Paranephrops* or *Astacopsis* in its general characters, but with the first pair of abdominal appendages fully formed, which we may call provisionally *Protastacus*, inhabited the ocean, and that it had as wide a distribution as *Palæmon* or *Penæus* have at the present day. Let us suppose, further, that the northern form of the genus tended towards the assumption of the Potamobiine, and the southern towards that of the Parastacine type. Under these circumstances, it is easy to understand how such rivers as were, or became, accessible in both hemispheres, and were not already too strongly tenanted by formidable competitors, might be peopled respectively by Potamobiine or Parastacine forms, which, acquiring their special characters in each great river-basin, would bring about the distribution we now witness. As time went on, the *Protastacus* stock might become extinct, or might be represented only by rare deep-water forms, as the Homaridæ are represented in the Indian Ocean only by *Nephropsis*.

Some such hypothesis as this appears to me to be fully justified by the present state of knowledge; and though it cannot as yet be said to be directly supported by palæontological facts, these facts agree with the hypothesis very well as far as they go. For the Mesozoic marine strata abound in Crustacea, such as *Glyphæa* and *Hoploparia*, which are evidently closely allied to the Crayfishes.

The great difficulty is, not to account for the Crayfishes where we find them, but to understand their absence over so large a part of the Old World and of intertropical America. Whether this is to be explained by extensive alterations in geographical conditions since the extinction of the *Protastacus* stock, or by the competition of Prawns and fresh-water Crabs, or by some other circumstance at present unknown, is a very interesting subject for further inquiry.

[1] G. O. Sars, 'Histoire Naturelle des Crustacés d'eau douce de Norvége.' In the British Museum there is a species of that especially marine genus *Penæus*, which is affirmed by the Messrs. Schlagintweit to have been obtained from an affluent of the Sutlej, at the foot of the Himalayas. *Penæus brasiliensis* ascends the North American rivers for long distances (Smith, in Prof. Baird's Report, 1872–73).

Postscript, Oct. 24, 1878.

Since this paper was read, my friend Mr. Moseley, F.R.S., has written for and obtained specimens of the "Crayfish" said to exist in the fresh waters of the Cape Verd Islands. They belong to the genera *Atya* and *Palæmon*. Moreover, by the intervention of Sir Joseph Hooker, I have procured a considerable number of fresh-water Crustacea from Jamaica. But these also all belong to *Atya* and *Palæmon*. I suspect that all Sloane's "Crayfishes" are simply Prawns. The largest example of one of the species sent to me measures sixteen inches in length when the great chelate limbs are fully extended.—T. H. H.

XVII

THE PRESIDENT'S ADDRESS

The Journal of the Quekett Microscopical Club, vol. v., 1878–9, *pp.* 144, 145.
(*Delivered November 22nd*, 1878.)

THE President said that the subject which he wished to bring before them that evening was a sort of contrivance which he had recently adopted himself, for the purpose of making dissections. They would all be aware that in a microscope to be used for delicate dissections, certain qualifications were absolutely essential. In the first place they must have perfect steadiness, the stand must be firmly and well supported, and be of sufficient strength and weight to bear the pressure put upon it without moving. Next it must be of convenient height, so that in working the hands might get a steady support; it should fulfil these two conditions, and yet not be so large as to be clumsy. The next point was as to the lenses; they should be of such a form as to give a maximum of power, and yet at the same time afford sufficient distance between them and the object to admit of needles being moved freely to an angle of 60° with the surface of the plate, because the efficiency of the needles obviously depended upon the angle at which they could be used, and if a lens were made with a wide face it would very often interfere with the movements of the needles. Then there was another point of still greater importance—when a careful dissection had been made, it often became desirable to examine it with a much higher power than the one which had served the purpose of preparation, and provision ought to be made to enable as high a power as was desired to be brought to bear without disturbing the object, and this could only be done by placing a compound body above the simple lens. The President

then exhibited the instrument which he had devised to meet these requirements, and pointed out that it consisted of a glass stage having a large aperture in the centre, and mounted horizontally upon three supports, one of which was formed by the pillar of the body; in this way it stood with great steadiness, and was strong enough to bear considerable pressure. The lens was carried by an arm projecting from the pillar, and made to turn aside horizontally when required; focussing and illumination were managed in the usual way, but there was a slow motion in addition to the rackwork. In offering the instrument for discussion, the question would arise as to the best form of lens to be employed, and he hoped to receive the opinions of the members upon this and other matters; but at present he used an ordinary low-power achromatic objective, made so as to slip into the arm without screwing; there was great convenience in thus mounting, and using a simple lens. With the old doublet there was much difficulty in working comfortably, and whether a person could do so or not depended a good deal upon his nose, being specially troublesome in the case of those persons who had somewhat aspiring noses. In addition to the lens which he had placed upon the instrument there was another belonging to it of half the focal length. Now, supposing they had made their dissection successfully, the point was how to be able to convert the instrument at once into a compound microscope without disturbing either the lens or the object. One of his aims in life had been to get microscope makers to abolish screws, which he regarded altogether as abominable inventions, and in this instance, the compound body had been made to slip over the outside of the socket in which the objective had been placed. This plan answered fairly well, but he thought it would be better to have it made to fit rather more easily, and to be secured by a bayonet joint, because, supposing that the power employed was not sufficient for the purpose, then inconvenience arose unless the body could be got off again with sufficient ease to ensure the object remaining undisturbed by any jerk or movement. With the improvement of the bayonet joint, it would be easy to remove the body, and having taken out the first lens and dropped in, say a one-eighth in., the body would go on again without any disturbance. He had the instrument before them made upon that pattern, to see how the thing would work; he had used it for the past six or eight months incessantly, and could certainly say that for his requirements it was the best thing he had seen, and he believed that with the little addition of a bayonet joint it would be as nearly perfect as any instrument of the kind could well be. He

thought that all persons who had been occupied in making minute dissections would see that it had value, and met all the requirements of the most delicate work. He hoped that the members would examine and criticise it, and make any suggestions that occurred to them for its further improvement, for it was becoming of very great importance to examine thin sections and minute portions of dissections without subjecting them to any such disturbance as to cause the slightest alteration, and it was equally important to be able to bring to bear upon them under such conditions the highest powers that might be needed.

XVIII

WILLIAM HARVEY

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ON the coming First of April, three hundred years will have elapsed, since the birth of William Harvey, who is popularly known as the discoverer of the circulation of the blood.

Many opinions have been held respecting the exact nature and value of Harvey's contributions to the elucidation of the fundamental problem of the physiology of the higher animals; from those which deny him any merit at all—indeed, roundly charge him with the demerit of plagiarism—to those which enthrone him in a position of supreme honour among great discoverers in science. Nor has there been less controversy as to the method by which Harvey obtained the results which have made his name famous. I think it is desirable that no obscurity should hang around these questions; and I add my mite to the store of disquisitions on Harvey which this year is likely to bring forth, in the hope that it may help to throw light upon several points about which darkness has accumulated, partly by accident and partly by design.

Every one knows that the pulsation which can be felt or seen between the fifth and sixth ribs, on the left side of a living man, is caused by the beating of the heart; and that, in some way or other, the ceaseless activity of this organ is essential to life. Let it be arrested, and, instantaneously, intellect, volition, even sensation, are abolished, and the most vigorous frame collapses, a pallid image of death.

Every one, again, is familiar with those other pulsations which may be felt or seen, at the wrist, behind the inner ankle, or on the

temples ; and which coincide in number and are nearly simultaneous with those of the heart. In the region of the temples it is easy, especially in old people, to observe that the pulsation depends on the change of form of a kind of compressible branched structure which lies beneath the skin, and is termed an artery. Moreover, the least observant person must have noticed, running beneath the skin of various parts of the body, notably the hands and arms, certain other bluish-looking bands which do not pulsate, and which mark the position of structures somewhat like the arteries, which are called veins.

Finally, accidental wounds have demonstrated to all of us that the body contains an abundance of a warm red fluid—the blood. If the wound has traversed a vein, the blood flows in torrents from its interior, in an even stream; if it has involved an artery, the flow takes place by jerks, which correspond in interval with the pulsations of the artery itself and with those of the heart.

These are facts which must have been known ever since the time when men first began to attend to and reflect upon the every-day course of nature, of which we form a part. I doubt not, also, that butchers, and those who studied the entrails of animals for purposes of divination, must very early have noticed that both the arteries and the veins are disposed in the fashion of a tree, the trunk of which is close to the heart and connected with it, while the branches ramify all over the body. Moreover, they could not fail to observe that the heart contains cavities, and that some of these communicate with the stem of the arteries and some with the stem of the veins. Again, the regular rhythmical changes of form, which constitute the beating of the heart, are so striking in recently killed animals, and in criminals subjected to modes of punishment which once were common, that the demonstration that the heart is a contractile organ must have been very early obtained, and have thus afforded an unintentional experimental explanation of the cause of the pulsation felt between the ribs.

These facts constitute the foundation of our knowledge of the structure and functions of the heart and blood-vessels of the human and other higher animal bodies. They are to be regarded as parts of common knowledge, of that information which is forced upon us whether we desire to possess it or not; they have not been won by that process of seeking out the exact nature and the causal connection of phenomena, to the results of which the term science may properly be restricted.

Scientific investigation began when men went further, and,

impelled by the thirst for knowledge, sought to make out the exact structure of all these parts, and to comprehend the mechanical effects of their arrangement and of their activity.

The Greek mind had long entered upon this scientific stage, so far back as the fourth century before the commencement of our era. For, in the works attributed to Aristotle, which constitute a sort of encyclopædia of the knowledge of that time, there is evidence that the writer knows as much as has been mentioned, and he refers to the views of his predecessors. Two thousand two hundred years ago the sciences of anatomy and physiology existed, though they were as yet young and their steps tottered.

Aristotle's description of the heart is often cited as an example of his ignorance, but I think unjustly. However this may be, it is certain that, not long after his time, great additions were made to anatomical and physiological science. The Greek anatomists, exploring the structure of the heart, found that it contained two principal cavities, which we now call the ventricles, separated by a longitudinal partition, or septum: the one ventricle is on its left, the other on its right side. It was to the fleshy body which contains the ventricles that the ancients restricted the title of "heart." Moreover, there is another respect in which their terminology was so different from that of the moderns, that, unless we recollect that the facts may be just as accurately stated in their fashion as in ours, we are liable to fall into the mistake of supposing that they are blundering.[1] What they speak of as the auricles of the heart, we term the appendices of the auricles ; and what we call the auricles are, for the ancients, on the right side, a part of the great vein or vena cava, and, on the left side, a part of the arterial system—the root, in fact, of what they termed the arteria venosa. Thus they speak of the auricles as mere appendages, or dilatations, situated upon the arterial and venous trunks respectively, close to the heart ; and they always say that the vena cava and the arteria venosa open into the right and left ventricles respectively. And this was the basis of their classification of the vessels, for they held all those vessels which, in this sense, open into the right ventricle to be veins, and all those which open into the left ventricle to be arteries. But here a difficulty arose. They observed that the aorta, or stem of the arteries, and all the con-

[1] We say that the heart, in man and the higher animals, consists of two auricles and two ventricles ; and that each auricle has an appendix in the form of a pouch. We term the vessel which arises from the right ventricle the pulmonary artery, because it supplies the lungs with blood. Those vessels which bring away the blood from the lungs to the left auricle, we call the pulmonary veins.

spicuous branches which proceed from it to the body in general are very different from the veins; that they have much thicker walls and stand open when they are cut, while the thin-walled veins collapse. But the "vein" which connected the right ventricle and the lungs had the thick coat of an artery, while the "artery" which connected the left ventricle and the lungs had the thin coat of a vein. Hence they called the former the *vena arteriosa*, or artery-like vein, and the latter, the *arteria venosa*, or vein-like artery.

The vena arteriosa is what we call the pulmonary artery, the arteria venosa is our pulmonary vein; but in trying to understand the old anatomists it is essential to forget our nomenclature and to adopt theirs. With this precaution, and with the facts before our mind's eye, their statements will be found to be, in the main, exceedingly accurate.

About the year 300 B.C. a great discovery, that of the valves of the heart, was made by Erasistratus. This anatomist found around the opening by which the vena cava communicates with the right ventricle, three triangular membranous folds, disposed in such a manner as to allow any fluid contained in the vein to pass into the ventricle, but not back again. The opening of the vena arteriosa into the right ventricle is quite distinct from that of the vena cava; and Erasistratus observed that it is provided with three pouch-like, half-moon-shaped valves; the arrangement of which is such that a fluid can pass out of the ventricle into the vena arteriosa, but not back again. Three similar valves were found at the opening of the aorta into the left ventricle. The arteria venosa had a distinct opening into the same ventricle, and this was provided with triangular membranous valves, like those on the right side, but only two in number. Thus the ventricles had four openings, two for each; and there were altogether eleven valves, disposed in such a manner as to permit fluids to enter the ventricles from the vena cava and the arteria venosa respectively, and to pass out of the ventricles by the vena arteriosa and the aorta respectively, but not to go the other way.

It followed from this capital discovery, that, if the contents of the heart are fluid, and if they move at all, they can only move in one way; namely, from the vena cava, through the ventricle and towards the lungs, by the vena arteriosa, on the right side; and, from the lungs, by way of the arteria venosa, through the ventricle, and out by the aorta for distribution in the body, on the left side.

Erasistratus thus, in a manner, laid the foundations of the theory of the motion of the blood. But it was not given to him to get any

further. What the contents of the heart were, and whether they moved or not, was a point which could be determined only by experiment. And, for want of sufficiently careful experimentation, Erasistratus strayed into a hopelessly misleading path. Observing that the arteries are usually empty of blood after death, he adopted the unlucky hypothesis that this is their normal condition, and that during life, also, they are filled with air. And, it will be observed, that it is not improbable that Erasistratus' discovery of the valves of the heart and of their mechanical action strengthened him in this view. For, as the arteria venosa branches out in the lungs, what more likely than that its ultimate ramifications absorb the air which is inspired ; and that this air, passing into the left ventricle, is then pumped all over the body through the aorta, in order to supply the vivifying principle which evidently resides in the air ; or, it may be, of cooling the too great heat of the blood ? How easy to explain the elastic bounding feel of a pulsating artery by the hypothesis that it is full of air! Had Erasistratus only been acquainted with the structure of insects, the analogy of their tracheal system would have been a tower of strength to him. There was no *prima facie* absurdity in his hypothesis—and experiment was the sole means of demonstrating its truth or falsity.

More than four hundred years elapsed before the theory of the motion of the blood returned once more to the strait road which leads truthwards ; and it was brought back by the only possible method, that of experiment. A man of extraordinary genius, Claudius Galenus, of Pergamos, was trained to anatomical and physiological investigation in the great schools of Alexandria, and spent a long life in incessant research, teaching, and medical practice.[1] More than one hundred and fifty treatises from his pen, on philosophical, literary, scientific, and practical topics, are extant ; and there is reason to believe that they constitute not more than a third of his works. No former anatomist had reached his excellence, while he may be regarded as the founder of experimental physiology. And, it is precisely because he was a master of the experimental method, that he was able to learn more about the motions of the heart and of the blood than any of his predecessors ; and to leave to posterity a legacy of knowledge, which was not substantially increased for more than thirteen hundred years.

The conceptions of the structure of the heart and vessels, of their actions, and of the motion of the blood in them, which Galen entertained, are not stated in a complete shape in any one of his

[1] Galen was born in the year 131 A.D., and died in or about the year 201.

numerous works. But a careful collation of the various passages in which these conceptions are expressed, leaves no doubt upon my mind that Galen's views respecting the structure of the organs concerned were, for the most part, as accurate as the means of anatomical analysis at his command permitted; and that he had exact and consistent, though by no means equally just, notions of the actions of these organs, and of the movements of the blood.

Starting from the fundamental facts established by Erasistratus respecting the structure of the heart and the working of its valves, Galen's great service was the proof, by the only evidence which could possess demonstrative value, namely, by that derived from experiments upon living animals, that the arteries are as much full of blood during life as the veins are, and that the left cavity of the heart, like the right, is also filled with blood.

Galen, moreover, correctly asserted, though the means of investigation at his disposition did not allow him to prove the fact, that the ramifications of the vena arteriosa in the substance of the lungs communicate with those of the arteria venosa, by direct, though invisible, passages, which he terms anastomoses; and that, by means of these communications, a certain portion of the blood of the right ventricle of the heart passes through the lungs into the left ventricle. In fact, Galen is quite clear as to the existence of a current of blood through the lungs, though not of such a current as we now know traverses them. For, while he believed that a part of the blood of the right ventricle passes through the lungs, and even, as I shall show, described at length the mechanical arrangements by which he supposes this passage to be effected, he considered that the greater part of the blood in the right ventricle passes directly, through certain pores in the septum, into the left ventricle. And this was where Galen got upon his wrong track, without which divergence a man of his scientific insight must infallibly have discovered the true character of the pulmonary current, and not improbably have been led to anticipate Harvey.

But, even in propounding this erroneous hypothesis of the porosity of the septum, it is interesting to observe with what care Galen distinguishes between observation and speculation. He expressly says that he has never seen the openings which he supposes to exist, and that he imagines them to be invisible, by reason of their small size and their closure by the refrigeration of the heart, after death. Nevertheless, he cannot doubt their existence, partly because the septum presents a great number of pits which obviously lead into its substance as they narrow, and, as he is so fond of saying, "Nature

makes nothing in vain;" and, partly because the vena cava is so large in comparison with the vena arteriosa, that he does not see how all the blood poured into the ventricle could be got rid of, if the latter were its only channel.

Thus, for Galen, the course of the blood through the heart was—on the right side, *in* by the vena cava, *out* by the vena arteriosa and the pores of the septum; on the left side, *in* by the pores of the septum and by the arteria venosa, *out* by the aorta. What now becomes of the blood which, filling the vena arteriosa, reaches the lungs? Galen's views are perfectly definite about this point. The vena arteriosa communicates with the arteria venosa in the lungs by numerous connecting channels. During expiration, the blood which is in the lungs, being compressed, tends to flow back into the heart by way of the vena arteriosa; but it is prevented from doing so, in consequence of the closure of the semilunar valves. Hence, a portion of it is forced the other way, through the anastomoses into the arteria venosa; and then, mixed with "pneuma," it is carried to the left ventricle, whence it is propelled, through the aorta and its branches, all over the body.

Galen not only took great pains to obtain experimental proof that, during life, all the arteries contain blood and not air, as Erasistratus supposed; but he distinctly affirms that the blood in the left ventricle and in the arteria venosa is different from that in the right ventricle and in the veins, including the vena arteriosa; and that the difference between the two lies in colour heat, and the greater quantity of "pneuma" contained in arterial blood. Now this "pneuma" is something acquired by the blood in the lungs. The air which is inspired into these organs is a kind of aliment. It is not taken bodily into the venosa arteria and thence carried to the left ventricle to fill the arterial system, as Erasistratus thought. On the contrary, Galen repeatedly argues that this cannot be the case, and often refers to his experimental proofs that the whole arterial system is full of blood during life. But the air supplies a material kindred to the "pneuma," out of which and the blood the "pneuma" is concocted. Hence, the contents of the arteria venosa are largely composed of "pneuma," and it is out of the mixture of this with the blood which filters through the septum, that the bright "pneumatic" blood found in the arteries, and by them distributed over the body, is formed. The arteria venosa is a channel by which "pneuma" reaches the heart, but this is not its exclusive function; for it has at the same time, to allow of the passage of certain fuliginous and impure matters which the blood contains, in the opposite

direction; and, it is for this reason, that there are only two valves where the arteria venosa enters the ventricle. These not fitting quite tightly, allow of the exit of the fuliginous matters in question.

Modern commentators are fond of pouring scorn upon Galen, because he holds that the heart is not a muscle. But if what he says on this subject is studied with care and impartiality, and with a due recollection of the fact that Galen was not obliged to use the terminology of the nineteenth century, it will be seen that he by no means deserves blame, but rather praise, for his critical discrimination of things which are really unlike.

All that Galen affirms is that the heart is totally unlike one of the ordinary muscles of the body, not only in structure, but in being independent of the control of the will; and, so far from doubting that the walls of the heart are made up of active fibres, he expressly describes these fibres and what he supposes to be their arrangement and their mode of action. The fibres are of three kinds, longitudinal, transverse, and oblique. The action of the longitudinal fibres is to draw in, that of the circular fibres to expel, and that of the oblique fibres to retain, the contents of the heart. How Galen supposed the oblique fibres could execute the function ascribed to them, I do not know; but it is clear that he thought that the activity of the circular fibres increased, and that of the longitudinal fibres diminished, the size of the cavities which they surrounded. Nowadays we term an active fibre muscular; Galen did not, unless, in addition, it possessed the characters of voluntary muscle.

According to Galen, the arteries have a systole and diastole (that is, a state of contraction and a state of dilatation), which alternate with those of the ventricles, and depend upon active contractions and dilatations of their walls. This active faculty of the arteries is inherent in them, because they are, as it were, productions of the substance of the ventricles which possess these faculties; and it is destroyed when the vital continuity of the arteries with the heart is destroyed by section or ligature. The arteries fill, therefore, as bellows fill, not as bags are blown full.

The ultimate ramifications of the arteries open by anastomoses into those of the veins, all over the body; and the vivifying arterial blood thus communicates its properties to the great mass of blood in the veins. Under certain conditions, however, the blood may flow from the veins to the arteries, in proof of which Galen adduces the fact that the whole vascular system may be emptied by opening an artery.

The two ventricles, the auricles, the pulmonary vessels, and the aorta with its branches, are conceived by the Greek anatomist to be an apparatus superadded to the veins, which he regards as the essential foundation and the most important part of the whole vascular system. No portion of Galen's doctrines has been more sharply criticised than his persistent refusal to admit that the veins, like the arteries, take their origin in the heart, and his advocacy of the view that the *fons et origo* of the whole venous system is to be sought in the liver. Here, however, I must remark, that it is only those who are practically ignorant of the facts who can fail to see that Galen's way of stating the matter is not only anatomically justifiable, but that, until the true nature of the circulation was understood and physiological considerations overrode those based upon mere structure, there was much more to be said for it than for the opposite fashion.

Remembering that what we call the right auricle was, for Galen, a mere part of the vena cava, it is impossible not to be struck by the justice of his striking comparison of the vena cava to the trunk of a tree, the roots of which enter the liver as their soil, while the branches spread all over the body. Galen remarks that the existence of the vena portæ, which gathers blood from the alimentary canal, and then distributes it to the liver, without coming near the heart, is a fatal objection to the view of his opponents, that all the veins take their rise in the heart; and the argument is unanswerable, so far as the mere anatomical facts are concerned.

Nothing could have appeared more obvious to the early anatomists than that the store of nutriment carried by the vena portæ to the liver was there elaborated into blood; and then, being absorbed by the roots of the venous system, was conveyed by its branches all over the body. The veins were thus the great distributors of the blood; the heart and arteries were a superadded apparatus for the dispersion of a "pneumatized," or vivified portion of the blood through the arteries; and this addition of "pneuma," or vivification, took place in the gills of water-breathing animals and in the lungs of air-breathers. But, in the latter case, the mechanism of respiration involved the addition of a new apparatus, the right ventricle, to insure the constant flow of blood through these organs of "pneumatization."

Every statement in the preceding paragraphs can be justified by citations from Galen's works; and, therefore, it must be admitted that he had a wonderfully correct conception of the structure and disposition of the heart and vessels, and of the mode in which the

ultimate ramifications of the latter communicate, both in the body generally and in the lungs; that his general view of the functions of the heart was just; and that he knew that blood passes from the right side of the heart, through the lungs, to the left side, and undergoes a great change in quality, brought about by its relation with the air in the lungs, in its course. It is unquestionable, therefore, that Galen, so far, divined the existence of a "pulmonary circulation," and that he came near to a just conception of the process of respiration; but he had no inkling even of the systemic circulation; he was quite wrong about the perforation of the septum; and his theory of the mechanical causes of the systole and diastole of the heart and arteries was erroneous. Nevertheless, for more than thirteen centuries, Galen was immeasurably in advance of all other anatomists; and some of his notions, such as that about the active dilatation of the walls of the vessels, have been debated by physiologists of the present generation.

No one can read Galen's works without being impressed by the marvellous extent and diversity of his knowledge, and by his clear grasp of those experimental methods by which, alone, physiology can be advanced. It is pathetic to watch the gropings of a great mind like his around some cardinal truth, which he failed to apprehend simply because he had not in his possession the means of investigation, which, at this time, are in the hands of every student. I have seen learned disquisitions on the theme, Why did the ancients fail in their scientific inquiries? I know not what may be the opinion of those who are competent to judge of the labours of Euclid, or of Hipparchus, or of Archimedes; but I think that the question which will rise to the lips of the biological student, fresh from the study of the works of Galen, is rather, How did these men, with their imperfect appliances, attain so vast a measure of success? In truth, it is in the Greek world that we must seek, not only the predecessors, but the spiritual progenitors, of modern men of science. The slumbering aptitude of Western Europe for physical investigation was awakened by the importation of Greek knowledge and of Greek method; and modern anatomists and physiologists are but the heirs of Galen, who have turned to good account the patrimony bequeathed by him to the civilized world.

The student of the works of the anatomists and physiologists of modern Europe in the fifteenth and the beginning of the sixteenth centuries, will find that they were chiefly occupied in learning of their own knowledge what Galen knew. It is not strange, therefore, that they were overpowered by so vast a genius, and that

they allowed themselves to be enslaved by his authority, in a manner which he would have been the first to reprove. Versalius, the great reformer of anatomy, had a bitter struggle to carry on Galen's work, by showing where he had erred in expounding the structure of the human body, on the faith of observations made on the lower animals ; but it was not till the middle of the sixteenth century, that anything was done to improve on Galen's physiology, and especially to amend his doctrines concerning the movements of the heart and of the blood.

The first step in this direction is very generally ascribed to Michael Servetus, the unhappy man whose judicial murder by slow fire was compassed by John Calvin ; he being instigated thereto by theological antagonism, intensified by personal hatred ; and aided and abetted in his iniquity by the Protestant Churches of Switzerland. The whole story has recently been clearly and fully told by Dr. Willis,[1] and I refer to it only for the purpose of remarking, that the name and fame of Calvin's victim would probably have been as completely obliterated as his persecutor intended they should be, had it not happened that one or two copies of the 'Christianismi Restitutio,' the attempted publication of which was the immediate cause of Servetus's death, were saved from destruction.

Servetus was undoubtedly well acquainted with anatomy, inasmuch as he was demonstrator to Johannes Guinterus in the School of Paris, where he had Vesalius for his colleague ; and, in his later years, he practised as a physician. Hence it is not wonderful to find that the 'Christianismi Restitutio,' although essentially a farrago of scatterbrained theological speculations, contains much physiological matter. And it is in developing his conception of the relations between God and man, that Servetus wrote the well-known passages on which many have asserted his claim to the discovery of the course of the blood from the heart, through the lungs, and back to the heart ; or what is now termed the pulmonary circulation.

I have studied the passages in question with great care, and with every desire to give Servetus his due, but I confess I cannot see that he made much advance upon Galen.[2] As we have seen, Galen said

[1] Servetus and Calvin, by R. Willis, M.D., 1877.

[2] I cannot but think that Dr. Willis's natural affection for his hero has carried him too far when he says, "Had his Restoration of Christianity been suffered to get abroad and into the hands of anatomists, we can hardly imagine that the immortality which now attaches so truly and deservedly to the great name of Harvey would have been reserved for him." But within six years of Servetus's death, the doctrine of the pulmonary circulation did get abroad through Realdus Columbus, without the effect supposed.

that some blood goes to the left side of the heart from the right side through the lungs, but that the greater part traverses the septum. Servetus appears, at first, to declare that all the blood of the right side goes through the lungs to the left side, and that the septum is imperforate. But he qualifies his assertion by admitting that some of the blood of the right ventricle may transude through the septum, and thus the question between him and Galen becomes merely one of degree. Servetus cites neither observation nor experiment in favour of the imperviousness of the septum; and the impression upon my mind is that he really knew no more than Versalius had already published, but that the tendency to headlong speculation, which is so characteristic of the man, led him to rush in where his more thoughtful colleague held back.

Whatever may be thought of the moral claim of Servetus to be regarded as the discover of the pulmonary circulation, there is no reason to believe that he had any influence on the actual progress of science.[1] For Calvin dealt with all the packages of the edition of the 'Christianismi Restitutio' he could lay hands on as he had served their author, and it is believed that only a few copies escaped the flames. One of these, in the National Library of France, is the very book used by the counsel for the prosecution, whom Calvin prompted, at Geneva; another is in Vienna. The public had no access to the work until it was reprinted, more than two centuries afterwards.

The first author who declared, without any qualification, that the septum of the ventricles is imperforate, and that all the blood of the right ventricle traverses the lungs and (except so much as may be retained for the nutrition of these organs) passes to the left ventricle, was Realdus Columbus, professor of anatomy in the famous school of Padua. The remarkable treatise, 'De Re Anatomica,' of this able anatomist, was published in 1559, or only six years after the death of Servetus, of whose notions there is no evidence that Columbus had any cognisance. Moreover, Columbus, as able an experimenter as he was a skilful dissector, deals with the question in a very different way from Servetus; so that, from his time, the existence of the pulmonary circulation, in the modern sense, may be said to have become established. Ambrose Paré, the great surgeon, writing in 1579,[2] refers to the course of the blood through the lungs as notoriously the discovery of Columbus. And I think not only that Realdus

[1] The arguments adduced by the learned and ingenious Tollin ("Die entdeckung der kreislaufs durch Michel Servet," 1876) on the other side, will hardly bear close scrutiny.

[2] The Works of Ambrose Parey, translated by Thomas Johnson, 1691, p. 97.

Columbus is entitled to the whole credit of this very considerable advance upon Galen's views; but that he is the only physiologist, between the time of Galen and that of Harvey, who made any important addition to the theory of the circulation.

The claim which is put forward on behalf of the celebrated botanist, Cæsalpinus, appears to me to be devoid of any foundation.[1] Many years after the publication of the work of Realdus Columbus, who was professor at the most famous and most frequented anatomical school of the time, and who assuredly was the last man to hide his light under a bushel, Cæsalpinus incidentally describes the pulmonary circulation in terms which simply embody a statement of Columbus's doctrine; adding nothing, and, to his credit be it said, claiming nothing. Like all the rest of the world since venesection was invented, Cæsalpinus noticed that the vein swells on the side of the ligature away from the heart; and he observes that this is inconsistent with the received views of the motion of the blood in the veins. If he had followed up the suggestion thus made to him by the needful experimental investigation, he might have anticipated Harvey; but he did not.

Again, Cannani discovered the existence of valves in some of the veins in 1547; and Fabricius rediscovered them, and prominently drew attention to their mechanism, in 1574. Nevertheless, this discovery, important as it was, and widely as it became known, had absolutely no effect in leading either the discoverers or their contemporaries to a correct view of the general circulation. In common with all the anatomists of the sixteenth century, Fabricius believed that the blood proceeded from the main trunk, or vena cava, outwards to the smallest ramifications of the veins, in order to subserve the nutrition of the parts in which they are distributed; and instead of being led by the mechanical action of the valves to reverse his theory of the course of the venous blood, he was led by the dominant theory of the course of the blood to interpret the meaning of the valvular mechanism. Fabricius, in fact, considered that the office of the valves

[1] "Videmus Cæsalpinum eadem de sanguinis itinere per pulmonem, atque de valvularum usu quæ Columbus ante docuisset proponere; causas vero sanguinis movendi juxta cum ignarissimis nescivisse; motus cordis atque arteriarum perturbasse; sanguinem e dextro cordis ventriculo per pulmonem in sinistrum ventriculum deferri, nullo experimento sed ingenii commento probabili persuasum credidisse. De venis ab injecto vinculo intumescentibus aliena omnino dixisse; alimentum auctivum e venis in arterias, per oscula mutua vasorum sibi invicem commissorum, elicitum invita experientia docuisse."

Not one of the ingenious pleaders for Cæsalpinus has yet, in my judgment, shown cause for the reversal of the verdict thus delivered by the learned biographer of Harvey in the edition of his 'Opera Omnia,' which was published by the College of Physicians in 1766.

was to break the impetus of the venous blood, and to prevent its congestion in the organs to which it was sent ; and, until the true course of the blood was demonstrated, this was as likely an hypothesis as any other.

The best evidence of the state of knowledge respecting the motions of the heart and blood in Harvey's time is afforded by those works of his contemporaries which immediately preceded the publication of the 'Exercitatio Anatomica,' in 1628.[1] And none can be more fitly cited for this purpose than the 'De Humani Corporis Fabrica, Libri decem,' of Adrian van den Spieghel, who, like Harvey, was a pupil of Fabricius of Aquapendente, and was of such distinguished ability and learning that he succeeded his master in the chair of anatomy of Padua.

Van den Spieghel, or Spigelius, as he called himself, in accordance with the fashion of those days, died comparatively young in 1625, and his work was edited by his friend Daniel Bucretius, whose preface is dated 1627. The accounts of the heart and vessels, and of the motion of the blood, which it contains, are full and clear ; but, beyond matters of detail, they go beyond Galen in only two points ; and with respect to one of these, Spigelius was in error.

The first point is the "pulmonary circulation," which is taught as Columbus taught it nearly eighty years before. The second point is, so far as I know, peculiar to Spigelius himself. He thinks that the pulsation of the arteries has an effect in promoting the motion of the blood contained in the veins which accompany them. Of the true course of the blood as a whole, Spigelius has no more suspicion than had any other physiologist of that age, except William Harvey ; no rumour of whose lectures at the College of Physicians, commenced six years before Spieghel's death, was likely in those days of slow communication and in the absence of periodical publications to have reached Italy.

Now let any one familiar with the pages of Spigelius take up Harvey's treatise and mark the contrast.

The main object of the 'Exercitatio' is to put forth and demonstrate, by direct experimental and other accessory evidence, a pro-

[1] The whole title of the copy of the rare first edition in the library of the College o. Physicians runs, "Exercitatio Anatomica de motu cordis et sanguinis in animalibus. Gulielmi Harvæi, Angli Medici Regii et Professoris Anatomiæ in Collegio Medicorum Londinensi. Francofurti, sumptibus Gulielmi Fitzeri. Anno MDCXXVIII." The dedications, of which that to Charles I. is pasted in, as if it had been an afterthought, extend to p. 9; the Procemium to p. 19; while the Exercitatio itself occupies pp. 20 to 72 inclusively. There are two plates illustrative of experiments on the veins of the arm.

position which is far from being even hinted at, either by Spigelius, or by any of his contemporaries or predecessors ; and which is in diametrical contradiction to the views respecting the course of the blood in the veins which are expounded in their works.

From Galen to Spigelius, they one and all believed that the blood in the vena cava and its branches flows from the main trunk towards the smallest ramifications. There is a similar consensus in the doctrine, that the greater part, if not the whole, of the blood thus distributed by the veins is derived from the liver; in which organ it is generated out of the materials brought from the alimentary canal by means of the vena portæ. And all Harvey's predecessors further agree in the belief that only a small fraction of the total mass of the venous blood is conveyed by the vena arteriosa to the lungs and passes by the arteria venosa to the left ventricle, thence to be distributed over the body by the arteries. Whether some portion of the refined and " pneumatic arterial blood traversed the anastomotic channels, the existence of which was assumed, and so reached the systemic veins ; or whether, on the contrary, some portion of the venous blood made its entrance by the same passages into the arteries, depended upon circumstances. Sometimes the current might set one way, sometimes the other.

In direct opposition to these universally received views, Harvey asserts that the natural course of the blood in the veins is from the peripheral ramifications towards the main trunk ; that the mass of the blood to be found in the veins at any moment was, a short time before, contained in the arteries, and has simply flowed out of the latter into the veins ; and finally that the stream of blood which runs from the arteries into the veins is constant, continuous, and rapid.

According to the view of Harvey's predecessors[1] the veins may be compared to larger and smaller canals, fed by a spring which trickles into the chief canals whence the water flows to the rest. The heart and lungs represent an engine set up in the principal canal to aërate some of the water and scatter it all over the garden. Whether any of this identical water came back to the engine or not would be a matter of chance, and it would certainly have no sensible effect on the motion of the water in the canals. In Harvey's conception of the matter, on the other hand, the garden is watered by channels so arranged as to form a circle, two points of which are occupied by propulsive engines. The water is kept moving in a continual round

[1] See the comparison of the veins to the canals for irrigating a garden in Galen, 'De Naturalibus Facultatibus,' vol. iii. cap. xv.

within its channels, as much entering the engines on one side, as leaves them on the other; and the motion of the water is entirely due to the engines.

It is in conceiving the motion of the blood, as a whole, to be circular, and in ascribing that circular motion simply and solely to the contractions of the walls of the heart, that Harvey is so completely original. Before him, no one, that I can discover, had ever so much as dreamed that a given portion of blood contained, for example, in the right ventricle of the heart, may, by the mere mechanical operation of the working of that organ, be made to return to the very place from which it started, after a long journey through the lungs and through the body generally. And, it should be remembered, that it is to this complete circuit of the blood, alone, that the term "circulation" can, in strictness, be applied. It is of the essence of a circular motion that that which moves returns to the place from whence it started. Hence, the discovery of the course of the blood from the right ventricle, through the lungs, to the left ventricle was in nowise an anticipation of the discovery of the circulation of the blood. For the blood which traverses this part of its course no more describes a circle, than the dweller in a street who goes out of his own house and enters his next-door neighbour's does so. Although there may be nothing but a party wall between him and the room he has just left, it constitutes an efficient *défense de circuler*. Thus, whatever they may have known of the so-called pulmonary circulation, to say that Servetus, or Columbus, or Cæsalpinus deserves any share of the credit which attaches to Harvey appears to me to be to mistake the question at issue.

It must further be borne in mind, that the determination of the true course taken by the whole mass of the blood is only the most conspicuous of the discoveries of Harvey; and that his analysis of the mechanism by which the circulation is brought about is far in advance of anything which had previously been published. For the first time, it is shown that the walls of the heart are active only during its systole or contraction, and that the dilatation of the heart, in the diastole, is purely passive. Whence it follows, that the impulse by which the blood is propelled is a *vis à tergo*, and that the blood is not drawn into the heart by any such inhalent or suctorial action, as not only the predecessors, but many of the successors of Harvey imagined it to possess.

Harvey is no less original in his view of the cause of the arterial pulse. In contravention of Galen and of all other anatomists up to his own time, he affirms that the stretching of the arteries which gives

rise to the pulse is not due to the active dilatation of their walls, but to their passive distension by the blood which is forced into them at each beat of the heart; reversing Galen's dictum, he says that they dilate as bags and not as bellows. This point of fundamental, practical as well as theoretical, importance is most admirably demonstrated, not only by experiment, but by pathological illustrations.

One of the weightiest arguments in Harvey's demonstration of the circulation is based upon the comparison of the quantity of blood driven out of the heart, at each beat, with the total quantity of blood in the body. This, so far as I know, is the first time that quantitative considerations are taken into account in the discussion of a physiological problem. But one of the most striking differences between ancient and modern physiological science, and one of the chief reasons of the rapid progress of physiology in the last half-century, lies in the introduction of exact quantitative determinations into physiological experimentation and observation. The moderns use means of accurate measurement, which their forefathers neither possessed nor could conceive, inasmuch as they are products of mechanical skill of the last hundred years, and of the advance of branches of science which hardly existed, even in germ, in the seventeenth century.

Having attained to a knowledge of the circulation of the blood, and of the conditions on which its motion depends, Harvey had a ready deductive solution for problems which had puzzled the older physiologists. Thus the true significance of the valves in the veins became at once apparent. Of no importance while the blood is flowing in its normal course towards the heart, they at once oppose any accidental reversal of its current, which may arise from the pressure of adjacent muscles, or the like. And, in like manner, the swelling of the veins on the further side of the ligature, which so much troubled Cæsalpinus, became at once intelligible, as the natural result of the damming up of the returning current.

In addition to the great positive results which are contained in the treatise which Harvey modestly calls an 'Exercise'; and which is, in truth, not so long as many a pamphlet about some wholly insignificant affair; its pages are characterized by such precision and simplicity of statement, such force of reasoning, and such a clear comprehension of the methods of inquiry and of the logic of physical science, that it holds a unique rank among physiological monographs. Under this aspect, I think I may fairly say that it has rarely been equalled and never surpassed.

Such being the state of knowledge among his contemporaries, and such the immense progress effected by Harvey, it is not wonderful that the publication of the 'Exercitatio' produced a profound sensation. And the best indirect evidence of the originality of its author, and of the revolutionary character of his views, is to be found in the multiplicity and the virulence of the attacks to which they were at once subjected.

Riolan, of Paris, had the greatest reputation of any anatomist of those days, and he followed the course which is usually adopted by the men of temporary notoriety towards those of enduring fame. According to Riolan, Harvey's theory of the circulation was not true; and besides that, it was not new; and, furthermore, he invented a mongrel doctrine of his own, composed of the old views with as much of Harvey's as it was safe to borrow, and tried therewith to fish credit for himself out of the business. In fact, in wading through these forgotten controversies, I felt myself quite at home. Substitute the name of Darwin for that of Harvey, and the truth that history repeats itself will come home to the dullest apprehension. It was said of the doctrine of the circulation of the blood that nobody over forty could be got to adopt it; and I think I remember a passage in the 'Origin of Species,' to the effect that its author expects to convert only young and flexible minds.

There is another curious point of resemblance in the fact, that even those who gave Harvey their general approbation and support sometimes failed to apprehend the value of some of those parts of his doctrine, which are, indeed, merely auxiliary to the theory of the circulation, but are only a little less important than it. Harvey's great friend and champion, Sir George Ent, is in this case; and I am sorry to be obliged to admit that Descartes falls under the same reprehension.

This great philosopher, mathematician, and physiologist, whose conception of the phenomena of life as the results of mechanism is now playing as great a part in physiological science as Harvey's own discovery, never fails to speak with admiration, as Harvey gratefully acknowledges, of the new theory of the circulation. And it is astonishing, I had almost said humiliating, to find that even he is unable to grasp Harvey's profoundly true view of the nature of the systole and the diastole, or to see the force of the quantitative argument He adduces experimental evidence against the former position, and is even further from the truth than Galen was, in his ideas of the physical cause of the circulation.

Yet one more and a last parallel. In spite of all opposition, the

doctrine of the circulation propounded by Harvey was, in its essential features, universally adopted within thirty years of the time of its publication. Harvey's friend, Thomas Hobbes, remarked that he was the only man, in his experience, who had the good fortune to live long enough to see a new doctrine accepted by the world at large. Mr. Darwin has been even more fortunate, for not twenty years have yet elapsed since the publication of the 'Origin of Species'; and yet there is no denying the fact that the doctrine of evolution, ignored, or derided, and vilified in 1859, is now accepted, in one shape or other, by the leaders of scientific thought in every region of the civilised world.

I proposed at the outset of this essay to say something about the method of inquiry which Harvey pursued, and which guided him throughout his successful career of discovery.

It is, I believe, a cherished belief of Englishmen, that Francis Bacon, Viscount St. Albans, and sometime Lord Chancellor of England, invented that "Inductive Philosophy" of which they speak with almost as much respect as they do of Church and State; and that, if it had not been for this "Baconian induction," science would never have extricated itself from the miserable condition in which it was left by a set of hair-splitting folk, known as the ancient Greek philosophers. To be accused of departing from the canons of the Baconian philosophy is almost as bad as to be charged with forgetting your aspirates; it is understood as a polite way of saying that you are an entirely absurd speculator.

Now the 'Novum Organon' was published in 1620, while Harvey began to teach the doctrine of the circulation in his public lectures, in 1619. Acquaintance with the "Baconian induction," therefore, could not have had much to do with Harvey's investigations. The 'Exercitatio,' however, was not published till 1628. Do we find in it any trace of the influence of the 'Novum Organon'? Absolutely none. So far from indulging in the short-sighted and profoundly unscientific depreciation of the ancients in which Bacon indulges, Harvey invariably speaks of them with that respect, which the faithful and intelligent study of the fragments of their labours that remain to us, must inspire in every one who is practically acquainted with the difficulties with which they had to contend, and which they so often mastered. And, as to method, Harvey's method is the method of Galen, the method of Realdus Columbus, the method of Galileo, the method of every genuine worker in science either in the past or the present. On the other hand, judged strictly by the standard of his

own time, Bacon's ignorance of the progress which science had up to that time made, is only to be equalled by his insolence towards men in comparison with whom he was the merest sciolist. Even when he has some hearsay knowledge of what has been done, his want of acquaintance with the facts and his abnormal deficiency in what I may call the scientific sense, prevent him from divining its importance. Bacon could see nothing remarkable in the chief contributions to science of Copernicus, or of Kepler, or of Galileo; Gilbert, his fellow countryman, is the subject of a sneer; while Galen is bespattered with a shower of impertinences, which reach their climax in the epithets "puppy" and "plague." [1]

I venture to think that if Francis Bacon, instead of spending his time in fabricating fine phrases about the advancement of learning, in order to play, with due pomp, the part which he assigned to himself of "trumpeter" of science, had put himself under Harvey's instruction, and had applied his quick wit to discover and methodise the logical process which underlaid the work of that consummate investigator, he would have employed his time to better purpose; and, at any rate, would not have deserved the just but sharp judgment which follows: "that his [Bacon's] method is impracticable cannot I think be denied, if we reflect, not only that it never has produced any result, but also that the process by which scientific truths have been established cannot be so presented as even to appear to be in accordance with it." I quote from one of Mr. Ellis's contributions to the great work of Bacon's most learned, competent, and impartial biographer, Mr. Spedding.[2]

Few of Harvey's sayings are recorded, but Aubrey[3] tells us that some one having enlarged upon the merits of the Baconian philosophy in his presence, "Yes," said Harvey, "he writes philosophy like a Chancellor." On which pithy reply diverse persons will put diverse interpretations. The illumination of experience may possibly tempt a modern follower of Harvey to expound the dark saying thus: "So

[1] "Video Galenum, virum angustissimi animi, desertorem experientiæ et vanissimum causatorem. . . . . O canicula! O pestis!—Temporis Partus Masculus!"

"Canicula" has even a coarser meaning than "puppy."

[2] General Preface to the Philosophical Works, vol. i. p. 38.

[3] Aubrey says: "He had been physitian to the Lord Ch. Bacon, whom he esteemed much for his witt and style, but would not allow to be a great philosopher. Said he to me, 'He writes philosophy like a L[d]. Chancellor,' speaking in derision . . . . He was very communicative, and willing to instruct any that were modest and respectful to him. And in order to my journey dictated to me what to see, what company to keep, what bookes to read, how to manage my studyes: in short, he bid me go to the fountaine head, and read Aristotle, Cicero, Avicenna, and did call the Neoteriques" —something almost as bad as "canicula": the little swarthy, black-eyed, choleric man.

this servile courtier, this intriguing politician, this unscrupulous lawyer, this witty master of phrases, proposes to teach me my business in the intervals of his. I have borne with Riolan, let me also be patient with him;" at any rate, I have no better reading to offer.

In the latter half of the sixteenth and the beginning of the seventeenth centuries, the future of physical science was safe enough in the hands of Gilbert, Galileo, Harvey, Descartes, and the noble army of investigators who flocked to their standard, and followed up the advance of their leaders. I do not believe that their wonderfully rapid progress would have been one whit retarded if the 'Novum Organon' had never seen the light: while, if Harvey's little 'Exercise' had been lost, physiology would have stood still until another Harvey was born into the world.

There is another point in reference to method on which I desire to contribute my mite towards the dissipation of a widespread popular delusion. On the faith of a conversation reported by Robert Boyle, Harvey is said to have declared that he discovered the circulation of the blood by reasoning deductively from the disposition of the valves of the veins. On this I may remark, firstly, that the words imputed to Harvey by no means warrant this conclusion; secondly, that if they did, the statement could not be true, because we have Harvey's own evidence to the contrary; and thirdly, that if the conclusion were warranted by the words reported, and were not contradicted by Harvey himself, it would still be worthless, because it is impossible to prove the circulation of the blood from any such data. What Robert Boyle says is this:—"And I remember that when I asked our famous Harvey in the only discourse I had with him (which was but a while before he died), what were the things that induced him to think of a circulation of the blood? he answered me, that when he took notice that the valves in the veins of so many parts of the body were so placed, that they gave free passage to the blood towards the heart, but opposed the passage of the venal blood the contrary way: he was invited to imagine that so provident a cause as nature had not so placed so many valves without design; and no design seemed more probable, than that since the blood could not well, because of the interposing valves, be sent by the veins to the limbs, it should be sent through the arteries and return through the veins, whose valves did not oppose its course that way." [1]

I have no doubt that it may be quite true, that Harvey was

[1] "A Disquisition about the Final Causes of Natural Things."—Boyle's Works, vol. v. p. 427.

"induced" to "think of a circulation of the blood" by considering the disposition of the valves of the veins; just as Cæsalpinus might have been led to the same thought; and then might have found out the true state of the case, if he had taken the hints which Nature gave him, and had used the proper means of investigation in order to discover whether those hints were valuable or worthless. Harvey must have learned the views of his master Fabricius; and it is likely enough that to his acute mind Fabricius's explanation of the functions of the valves seemed rather lame. But, as a matter of fact, Harvey did not reason out the circulation from the datum of the valves. On this point his own words, in the passage which contains the fullest account of the considerations which led him to the doctrine of the circulation, leave no doubt whatever: —

"Thus far I have spoken of the passage of the blood from the veins into the arteries,[1] and of the manner in which it is transmitted and distributed by the action of the heart; and thus far some, perhaps, moved by the authority of Galen, or of Columbus, or by the reasonings of other authors, will agree with me. But when I proceed to what remains to be said concerning the quantity and the origin of the blood thus transmitted (though it is highly worthy of consideration) it will seem so new and unheard of, that I not only fear injury to myself from the envy of a few; but I dread lest I make all mankind my enemies. So much does custom, or teaching once accepted and fixed by deep roots, weigh with all; and such is the influence of the venerable opinion of antiquity. However this may be, now that the die is cast, my hope lies in the candour of lovers of truth and of learned minds. Indeed, when I thought often and seriously upon how large the quantity [of transmitted blood] is; upon my dissections of living animals (for the purposes of experiment) and the opening of arteries and the many considerations arising therefrom; as well as upon the magnitude and the symmetry of the ventricles of the heart and of the vessels which enter and leave them (since nature makes nothing in vain, so great a size proportionally would not be given to these vessels without an object); and upon the elaborate mechanism of the valves and fibres, and of the rest of the structure of the heart; as well as of many other things; and when I long turned over in my mind, what might be the quantity of the transmitted

[1] In the preceding chapter (vii.) Harvey has been discussing the passage of the blood through the lungs, supporting his views, among other arguments, by the authority of Galen and of Columbus; and it must be remembered that he termed the pulmonary artery *vena arteriosa*, and the pulmonary vein *arteria venosa*. Wherefore he properly speaks of the passage of the blood "from the veins into the arteries."

blood; in how short a time its transmission might be effected; whether that quantity could be supplied by the juices of the food ingested; I came at length to the conclusion that the veins would become collapsed and empty, while the arteries, on the other hand, would be ruptured, by the excess of blood poured into them; unless there were some road by which the blood could at length run back from the arteries into the veins and return to the right ventricle of the heart. So I began to think whether there was a kind of motion as it were in a circle; this I afterwards found to be true."[1]

In all this very full and interesting account of the course of Harvey's inquiry, it will be observed that not one word is said about the valves of the veins. The valves of which he speaks are those of the heart, which had been known, as I have pointed out, ever since the days of Erasistratus.

Finally, I venture to affirm that Harvey did not deduce the circulation from the disposition of the valves of the veins, because it is logically impossible that any such conclusion should be deduced from such premisses. The only conclusion which is warranted by the presence of valves in the veins is, that such valves will tend to place a certain amount of obstacle in the way of a liquid flowing in a direction opposite to that in which the valves are inclined. The amount of obstacle, from mere impediment to absolute barring of the way, will depend upon the form and disposition of the valves; upon their inertia, or stiffness of motion, in relation to the force of the current of liquid; and, above all, upon the firmness or yieldingness of the walls of the tube to which they are attached. The valve which hermetically closes the passage through an iron pipe may be of no use in an india-rubber tube. Therefore, unless the action of such valves as exist in the veins were carefully tested by experiment on the living animal, any conclusions that might be based upon their presence would be of doubtful value, and might be interpreted either in the sense of Fabricius, or in that of Harvey.

Moreover, supposing that it could be proved that, in those veins in which valves exist, the blood can move only in one way, what is to be said about the numerous veins which have no valves? And, unless we already know upon experimental grounds that the walls of the cavities of the heart contract in a certain definite order; that the arteries are full of blood and not of air; and a number of other important facts which can only be experimentally determined; what good is it to know that there are valves in the veins? There are

[1] Gulielmi Harveji. 'Exercitationes Anatomicæ.' Exercitatio I. cap. viii. ed. 1660.

valves in the lymphatics as well as in the veins, and yet any one who concluded therefrom that the lymph circulates after the manner of the blood would make a woeful mistake.

The fact is that neither in this, nor in any, physiological problem can mere deductive reasoning from dead structure tell us what part that structure plays, when it is a living component of a living body. Physiology attempts to discover the laws of vital activity, and these laws are obviously ascertainable only by observation and experiment upon living things.

In the case of the circulation of the blood, as in that of all other great physiological doctrines, take away the truths which have been learned by observation and experiment on living structures, and the whole fabric crumbles away. Galen, Columbus, Harvey, were all great vivisectors. And the final ocular demonstration of the circulation of the blood by Malpighi, seven years after Harvey's death—the keystone of the fabric he raised—involved an experiment on a living frog.

This experiment can be performed on a demonstrably insensible animal. Nevertheless, any English subject who repeats it, in these days, may be subjected to fine or imprisonment, as a common malefactor, whenever the chances of political strife give the Home Office to some minister of less knowledge, less justice, and, above all, less firmness in resisting open and underhand pressure, than the present Secretary of State for the Home Department.

I do not think the present is a fitting occasion for the discussion of the burning question of vivisection. My opinions on the subject have been formed and expressed under a due sense of responsibility, and they have not been, and are not likely to be, affected by the preposterous misrepresentations and unseemly abuse which they have evoked. The good Harvey, in one of his fits of choler, I suppose, said that "man was but a great mischievous baboon,"[1] and yet, for twenty years, he kept silence, and, at the end, answered Riolan with quite angelic mildness. I can imitate his silence, if not his mildness; and therefore I have nothing further to offer on this subject. It may be that those are right who say, perish the human race, rather than let a dog suffer. It may be that those are right who think that a man is worth a wilderness of apes, and that he who will not save human life when he could do so, by sacrificing a hecatomb of animals, is an accomplice in murder.

But without touching upon this debatable ground, I may be of some use in cleansing the ground of mere rubbish. I submit two

[1] Aubrey.

points for your consideration. The one of these is the unquestionable fact that physiology is based upon experiment and can only grow by experiment; and that the discovery of the true motion of the blood, which is one of the cardinal doctrines of that science, and a doctrine the truth of which is implied in the diagnosis and the treatment of nine diseases out of ten, has been made in no other way than by reasoning on the data supplied by repeated and multiplied vivisections.

The other is a mere suggestion, which, perhaps, may be dictated by a want of power on the part of a man who is growing old, to adjust himself to a changing world. The great mark of senility, I believe, is to be a " laudator temporis acti." But, as Harvey says, " the die is cast, and I put my faith in the candour of the lovers of truth and of learned minds."

I have had occasion to remark that the science of former days was not so despicable as some think; and that, however foolish undue respect for the wisdom of the ancients may be, undue disrespect for it may be still more reprehensible. Now I fancy that a candid mind will admit it to be within the limits of possibility, that the like may apply to the public opinion and the moral sense of former ages.

Harvey was the favoured friend of his sovereign, the honoured Nestor of his profession, the pride of his countrymen. If he lived now, and were guilty of serving mankind to the same extent and in the same way, so far from any such marks of favour reaching him, he would find himself to be a mark of a different kind—a mark, I mean, for immeasurable calumny and scandalous vituperation; and though his professional brethren would surely pay him all honour, so far from being the pride of his countrymen, a goodly number of them, of all grades in the social scale, would be spending a world of energy in the endeavour to give him the legal status of a burglar.

I venture to ask you to consider seriously whether, under these circumstances, it is quite so certain, as some seem to believe, that the public opinion of the England of Harvey's day—that time when Englishmen could hurl back a world arrayed in arms against them, because they feared neither to suffer, nor to inflict pain and death in a good cause; that age within which Shakespeare and Milton, Hobbes and Locke, Harvey and Newton, Drake and Raleigh, Cromwell and Strafford, embodied the powers of our race for good and evil in a fashion which has had no parallel before or since—was absolutely contemptible when set against that of this present enlightened and softly nurtured, not to say sentimental, age.

Maybe it is; possibly the world is entering upon a phase in which the recognised whole duty of man will be to avoid the endurance, or the infliction, of physical pain, whatever future alleviation of misery may be its consequence, however great the positive benefit to mankind which may flow thereupon. If so, "Finis Physiologiæ." When that time arrives, there will be an end to all progress in our knowledge of the laws of life, to all advance towards rational medicine. And, if I do not greatly err, these are not the only things which the logical outcome of such premisses will have abolished. Crime must go unpunished—for what justification is there for "torturing" a poor thief or murderer except the general good of society? The "voice of the sluggard" will not "be heard to complain," for no one will dare to "torture him by disturbing his slumbers." There will be no means of transport, and nothing to ride, except steam-engines, and bicycles, for the "torture" involved in the training and in the labour of beasts of draught and burden will be insufferable. No man will think of eating meat, though it may be proper for him to serve as meat to other creatures; for what right can men have to "torture" fleas by the administration of insecticide powder, merely for the benefit of mankind? Sport, I need not say, will have been abolished, and war will have followed it; not so much because war is fraught with evil for men but because of the awful "torture" which it inflicts directly upon horses and mules, to say nothing of the indirect dyspeptic sufferings of the vultures and wolves, which are tempted by our wickedness to overeat themselves.

As I have confessed, I find myself to be regrettably out of harmony with many worthy and enthusiastic people among my contemporaries; and perhaps the prospect of the coming of the New Era, in which these things shall be, does not affect others as it does me. To say truth, I am rather glad to think that the species can hardly be perfected thus far, in my time. I must distinctly admit that I should be loath to be obliged to exist in a world, in which my notions of what men should be and do will have no application. As the old Norseman said, when the choice between Heaven with the new generation, and Hell with the old, was offered him, "I prefer to be with my ancestors."

XIX

ON THE CHARACTERS OF THE PELVIS IN THE MAMMALIA, AND THE CONCLUSIONS RESPECTING THE ORIGIN OF MAMMALS WHICH MAY BE BASED ON THEM.

Proceedings of the Royal Society of London, vol. xxviii., 1879, *pp.* 395–405.
(*Read March 6th*, 1879.)

(PLATE 8 [PLATE 25].)

IN the course of the following observations upon the typical characters and the modifications of the pelvis in the Mammalia, it will be convenient to refer to certain straight lines, which may be drawn through anatomically definable regions of the pelvis, as *axes.* Of these I shall term a longitudinal line traversing the centre of the sacral vertebræ, the *sacral axis* (Plate 8 [Plate 25], *S. a.*); a second, drawn along the ilium, dorso-ventrally, through the middle of the sacral articulation and the centre of the acetabulum, will be termed the *iliac axis* (*Il. a.*); a third, passing through the junctions of the pubis and ischium above and below the obturator foramen, will be the *obturator axis* (*Ob. a.*); while a fourth, traversing the union of the ilium, in front with the pubis, and behind with the ischium, will be the *iliopectineal axis* (*Ip. a.*).

The least modified form of mammalian pelvis is to be seen, as might be expected, in the Monotremes, but there is a great difference between *Ornithorhynchus* and *Echidna* in this respect, the former being much less characteristically mammalian than the latter.

In *Ornithorhynchus* (Plate 8 [Plate 25], fig. 4), the ilium is remarkably narrow, and the angle between the iliac and the sacral axis is large, so that the ilium is but very slightly inclined backwards. The iliopectineal axis, nearly at right angles with the iliac axis, is inclined to the sacral axis at an acute angle; while the obturator

axis is nearly perpendicular to the sacral axis, and the obturator foramen is relatively small. The front margin of the cotyloid end of the pelvis sends off a very strong *pectineal process* (*p. p.*), from the inferior basal part of which a short, obtuse *tuberculum pubis* (*t. p.*) projects. Between this and the symphysis, the base of the marsupial bone (*Ep. p.*) is attached. The ventral rami of the pubes are short and, like those of the ischium, they are united throughout their whole length in a long symphysis, the ischial division of which (*Sy. I.*) is as long as, if not longer than, the pubic division (*Sy. p.*). The cotyloid ramus of each ischium gives off a stout elongated *metischial process* (*m. p.*) backwards.

In *Echidna* (Plate 8 [Plate 25], fig. 5), on the other hand, the ilium is much broader; while the iliac axis inclines downwards and backwards, at an acute angle with the sacral axis. The iliopectineal axis being still at right angles with the iliac axis, makes a much larger angle with the sacral axis; and the obturator axis is inclined from above, at an angle of nearly 45° to the sacral axis, downwards and backwards. In fact, the change in the general character of the pelvis seems to result from its ventral elements having been carried backwards and upwards by the backward and upward shifting of that portion of the ilium which lies below the level of its articulation with the sacrum. There are other changes by which the aspect of the pelvis is much altered. The inner wall of the acetabulum is incompletely ossified, but, in other respects, the pelvis makes a considerable approximation towards the ordinary mammalian form. Thus the pectineal process is represented by a less prominent and more elongated ridge; the metischial process widens out into a mere triangular expansion or "tuberosity," of the ischium, and the symphysial union of the ischia is short.

In all other Mammalia (*e.g.*, *Lepus*, Plate 8 [Plate 25], fig. 6), the iliac axis forms as acute, if not a more acute, angle with the sacral axis; the angle between the ilio pectineal axis and the sacral axis more and more approaches a right angle; and that between the sacral axis and the obturator axis becomes more and more acute. The obturator foramen acquires a much larger proportional size. The symphysial union becomes restricted to a greater or less portion of the pubes; or the ventral halves of the ossa innominata may cease to be directly united, even the pubes being far apart in the dry skeleton. The metischial processes are represented by tuberosities, which may extend upwards and unite with anterior caudal vertebræ; and the ilia may remain narrow or become extremely expanded. In all monodelphous Mammalia the marsupial bones disappear.

The distinctive features of the mammalian pelvis have been clearly indicated by Gegenbaur,[1] who points out that in mammals, in contradistinction from reptiles, "the longitudinal axis of the ilium gradually acquires an oblique direction, from in front and above, backwards and downwards. The part which represents the crista above thus becomes turned forwards, or more or less outwards, with increase of lateral surface; the acetabular part backwards and downwards; hence the ischium retains its original direction in the produced long axis of the ilium and, at the same time, takes up a position in relation to the vertebral column similar to that which obtains in birds. The conditions of this position are, however, to be sought in factors of a totally different nature in mammals from those which produce it in birds; for in the former, the ischium follows the changed direction of the ilium, whilst in birds, the ilium has nothing to do with the matter, and the ventral elements of the pelvis appear to pass towards the caudal region, independently of the ilium."

On one point, however, I cannot agree with Gegenbaur's conclusions. He is of opinion that the ilium of mammals answers to the post-acetabular part of the ilium of birds, and that "the *crista ossis ilii* of mammals corresponds with the posterior edge of the post-acetabular part of the bird's ilium. Between the two parts, therefore, there is the difference of a rotation through an angle of almost 180°." On the contrary, it appears to me evident that the whole *crista ilii* in a mammal corresponds with the whole dorsal edge of the ilium in a bird or a reptile, and that the angle through which the iliac axis rotates amounts to not more than 90° (compare Plate 8 [Plate 25], fig. 6, *Lepus*, with fig. 9, *Apteryx*). I cannot reconcile the contrary view either with the relations of the ilium to the sacrum, or with the attachment of the muscles.

On comparing the pelvis of *Ornithorhynchus* with that of a lizard (Plate 8 [Plate 25], fig. 2), or that of a Chelonian, it will be observed that the resemblance between the former and the Sauropsidan pelvis is, in most respects, closer than that which it bears to the higher Mammalian pelvis. In the reptiles both the pubes and the ischia unite in a ventral symphysis; the pubis has a strong pectineal process, which acquires very large dimensions in the *Chelonia*; the metischial processes are also often very strong. Nevertheless, there is an important difference, for, in all these animals, the iliac axis is either nearly perpendicular to the sacral axis, or slopes from above downwards and forwards; the obturator axis also inclines downwards

[1] "Beiträge zur Kenntniss des Beckens der Vögel," "Jenaische Zeitschrift," vi.

and forwards. Hence, in most *Lacertilia* and *Chelonia*, the pubes slope forwards very obliquely, while the ischia come more and more forwards. In other words, such modifications of the pelvis as occur in the Lacertilia and the Chelonia are of an opposite kind to those which take place in Mammalia.

The same thing is true of the *Crocodilia* (Plate 8 [Plate 25], fig. 3). Here the ilium is much broader than in the lizards and the *Chelonia*. This broadening is effected by the expansion of the ilium, both in front of and behind the iliac axis, which retains about the same inclination to the sacral axis that it has in lizards. The ischia have but small metischial processes, and their long axes lie further forwards than in most lizards. The obturator axis inclines forwards, and the iliopectineal axis is parallel with the sacral axis, as in lizards. As in *Echidna*, a space of the inner wall of the acetabulum is fibrous. The lower boundary of this space is constituted by a prolongation of the anterior end of the cotyloid extremity of the ischium. The interval between this and the anterior end of the ilium answers to the cotyloid end of the pubis in a lizard, but it does not ossify. The pubis corresponds exactly in direction with that of a lizard, but its form is very different. At first narrow and rounded, it gradually flattens from above downwards, and, at the same time, widens into a broad trowel-shaped plate of cartilage enclosed in a dense fibrous perichondrium, which lies close beside the middle line in the ventral wall of the abdomen (Plate 8 [Plate 25], fig. 12). Each of these flat cartilages is distinct from its fellow throughout the greater part of its extent; but, posteriorly, the two approach, and are united by a broad and strong ligamentous band (*Sy. p. l.*). The bony portion of the pubis commences just outside the acetabulum and extends to this band, terminating by a curved edge directed inwards and forwards. It is the osseous portions of the pubes which are commonly described as the entire pubes of the Crocodilia, and much speculative ingenuity has been expended upon the interpretation [1] of these apparently anomalous elements of the pelvis, which are readily moveable upon their fibro-cartilaginous connexions with the acetabulum. But in no essential respect do they differ from ordinary pubes. Throughout their whole length they give attachment to a muscle, which answers to the pectineus and short adductors of the

[1] For the latest of these interpretations see Hoffman's excellent memoir, "Beiträge zur Kenntniss des Beckens der Amphibien und Reptilien." "Nied. Archiv für Zoologie," 1876. I cannot but think that had Professor Hoffman studied the crocodile's pelvis in fresh or spirit specimens, he would not have put forward the hypothesis that the pubes of the crocodiles are "epipubes." Rathke's account of the development of the crocodile's pelvis affords conclusive evidence respecting the homologies of the pubes in these animals.

thigh, while the aponeurosis which lies between them and the ischia gives origin as usual to the obturator externus; and the obturator nerves pass out close to the cotyloid ends of the pubes (Plate 8 [Plate 25], fig. 12, *Ob. n.*). For the trowel-shaped forward continuations of the pubes on each side of the symphysis, I will adopt the name of *epipubes*, proposed by Hoffman for other structures which I believe to be homologous with them. They are firmly connected with the aponeurosis of the external oblique muscle, in which, just in front of their outer edges, lie, on each side, the first set of abdominal false ribs (Plate 8 [Plate 25], fig. 12, *r.*). In short, in all their most important relations, these appear to me to be structures homologous with the marsupial bones of the Monotremes and Marsupials, which in *Thylacinus* are represented by mere cartilages. But although homologous, they are very different in detail; and, in all other respects, the Crocodilian pelvis departs even further than that of the Chelonia and Lacertilia from the Mammalian type.

The *Pterosauria* seem to have possessed epipubes; and in the *Dicynodontia* there is an approximation to the backward elongation of the subsacral part of the ilium which is characteristic of Mammals; but, in both these groups there appears to have been no obturator fontanelle.

In the ornithoscelidan reptiles and in birds (Plate 8 [Plate 25], figs. 7, 8, and 9), the pelvis, starting from the lacertilian and crocodilian type, undergoes a series of modifications of a new character, the ultimate result of which is a pelvis as much specialised as that of the higher Mammals, but totally different from it in principle.

The broadening of the ilium seen in the crocodile increases, so that the antero-posterior length of the bone eventually becomes very great, chiefly in consequence of the elongation of the præaxial region of the ilium. But, with all this, the direction of the iliac axis does not sensibly change, and it remains more or less inclined downwards and forwards (Plate 8 [Plate 25], fig. 9). The inner wall of the acetabulum is largely membranous. The iliopectineal axis becomes slightly inclined to the sacral axis, but never so much even as in *Echidna*. The main change in the pelvis is, in fact, effected by the extraordinary elongation of the pubes and the ischia, and their rotation backwards and upwards; while, at the same time, the symphysial union of the bones of opposite sides altogether disappears. In *Rhea*, the ischia unite with some of the post-sacral vertebræ as they do in many Mammalia. The pubis becomes very slender and, as it lies parallel with the ischium, the obturator space is reduced to a

mere slit, often bridged over by a process of the ischium.[1] The pectineal process is immensely elongated in some Ornithoscelida (as Hulke has shown in *Iguanodon*, and Marsh in *Laosaurus* (Plate 8 [Plate 25], fig. 8); but, in birds, it is usually short (fig. 9), and may be absent, and no epipubes have been discovered, either in the Ornithoscelida or in birds.[2]

Thus it appears to be useless to attempt to seek among any known Sauropsida for the kind of pelvis which analogy leads us to expect among those vertebrated animals which immediately preceded the lowest known Mammalia. For, if we prolong the series of observed modifications of the pelvis in this group backwards, the "Promammalia" antecedent to the Monotremes may be expected to have the iliac and obturator axes perpendicular to the sacral axis, and the iliopectineal axis parallel with it; something, in short, between the pelvis of an *Ornithorhynchus* and that of a land tortoise; and provided, like the former, with large epipubes intermediate in character between those of the lower mammals and those of crocodiles. In fact, we are led to the construction of a common type of pelvis, whence all the modifications known to occur in the Sauropsida and in the Mammalia may have diverged.

It is a well-known peculiarity of the urodele Amphibia, that each *os innominatum* consists of a continuous cartilage, the ventral half of which is perforated by a foramen for the obturator nerve, but has no large fibrous fontanelle, or obturator foramen, in the ordinary sense of the word. At the junction of the dorsal with the ventral moiety, the acetabulum marks off the iliac portion of the pelvic arch above, from the pubic and ischial regions below; and these are further distinguishable, even apart from their ossifications, by the position of the foramen for the obturator nerve and the origins of the muscles. In full-grown specimens of *Salamandra maculosa*, the pelvis presents the following characters (Plate 8 [Plate 25], figs. 1, 10, and 11):—The iliac axis is slightly inclined forwards, while the iliopectineal axis is practically parallel with the sacral axis. The iliac ossification extends into the acetabulum, and forms a triangular segment of its roof with the apex downwards, exactly as in lizards. The posterior and inferior side of the triangle is separated by a thin band of the primitive cartilage from the upper edge of the similarly triangular

[1] I was, at one time, inclined to think that this represented the union of the pubes and ischia of the same side in ordinary *Sauropsida*, and that the rest of the ischium represented an unusually elongated metischial process; but the study of the development of the pelvis in the chick has convinced me that this is not the case.

[2] See, however, the observations of Mr. Garrod on a "marsupial bone" in ostriches. "Proceedings of the Zoological Society," 1872.

cotyloid end of the ischial ossification, the anterior edge of which is vertical, again as in lizards. Between this edge and the anterior and inferior edge of the iliac ossification there is a cartilaginous interspace, as in crocodiles, which represents the cotyloid end of the pubis (Plate 8 [Plate 25], fig. 1). This cartilaginous part of the pubis gives rise to a pectineal process (*p. p.*), which has the same position as in birds and in *Ornithorhynchus*. In the floor of the acetabulum, the pubic ossification (fig. 1, *Pb.*) makes its appearance as a very thin lamina, which extends, underneath the pectineal process, inwards; and gradually surrounds the whole of the thickened transverse ridge of cartilage which corresponds with the pubis. The pubis is thus represented by an axis of cartilage surrounded by bone, and the thick inner extremities of the two pubes are largely united by fibrous tissue (fig. 10, *Sy. p.*). The ischia are relatively large, and are united, partly by cartilage and partly by ligament, in a long symphysis (fig. 10, *Sy. I.*). Their posterior and external angles are produced into short metischial processes. In one specimen, I observed a distinct sutural line (Plate 8 [Plate 25], fig. 11, *s.*), between the anterior curved edge of the right ischium and the corresponding pubis, while no such suture could be traced upon the other side.

The pelvic arch of *Salamandra*, therefore, contains all the elements which are found in the higher Vertebrata, but the obturator fontanelle is wanting.

Proceeding from the symphysis pubis, with which it is connected by ligament, is the "ypsiloid" cartilage or epipubis (figs. 1, 11, *Ep. p.*), which was called by the accurate and acute Dugès the "marsupial cartilage." This indication of the homology of the part has been adopted by Cuvier and others, but I do not know that it has been generally accepted. I believe, however, that the identification is perfectly just.

The ypsiloid cartilage proceeds forwards in the middle line, as a stem (*Ep. p*). of variable length, and then divides into two branches (*Ep. p*[1]., *Ep. p*[2].), which diverge at right angles to one another, and terminate by rounded extremities. The pedicle of the ypsiloid cartilage is broad and triangular in section, the apex of the triangle being dorsal.

The manner in which the abdominal muscles are connected with this cartilage is very instructive (Plate 8 [Plate 25], figs. 13, 15). The anterior pectinations of the external oblique muscle (*O. e.*) are inserted into a thin but dense fascia, which is hardly separable from the superjacent dermis, and which extends across the middle line to the muscle of the other side. The most

posterior bundles of the external oblique, however, are inserted by a rounded tendon into the pectineal process (Plate 8 [Plate 25], fig. 15, *p. p.*), which therefore answers to the spine or tuberosity of the pubis in Mammalia. Internal to this, the fascia arches over a small space (*i. r.*) (which corresponds with the inguinal ring), and is then inserted into the whole length of the pedicle and into the posterior half of each ramus of the ypsiloid cartilage. Beyond this point the rami are free externally, though they lie close against the fascia. On their inner sides, however, they are connected together and with the fascia of the external oblique, in the middle line, by a delicate sheet of fibrous tissue (figs. 13 and 15, *f*). On comparing this disposition of the tendon of the external oblique muscle with that which obtains in *Ornithorhynchus* (Plate 8 [Plate 25], fig.] 14) the correspondence is obvious. For, in the latter, the posterior fibres of that muscle are inserted directly into the spine of the pubis (*t. p.*). Between these and the outer edge of the marsupial bone there is fibrous interspace, corresponding with the inguinal ring (*i. r.*); while the more anterior fibres of the external oblique are inserted into the apex of the bone, which is, as it were, imbedded in the fascia. If the pedicle of the ypsiloid cartilage were reduced, the rami at the same time widening behind, until their outer angles reached the pectineal processes, and their free apices shortening the ypsiloid cartilage of the salamander would be converted into two cartilages having exactly the same relation to the tendon of the external oblique that the marsupial bones have in the *Ornithorhynchus*.

In the Monotremes (Plate 8 [Plate 25], fig. 14, *Py.*), there are two very large pyramidales muscles, which spring from the whole inner margins of the marsupial bones; their posterior and middle fibres run to the middle line, but the anterior ones constitute a longitudinal band, which extends forwards, and is inserted along with the rectus (*R.*), of which, indeed, it looks like a part. In the salamander, muscular fibres similarly take their origin from the inner edges of the rami of the epipubis; and the most anterior of these fibres pass forwards, and become more or less confounded with the inner edges of the recti (fig. 13, *Py.*). But the region which answers to the *linea alba* (*l. a.*) is very broad, whence the pyramidales are separated by a wide interval.

Thus far, the muscles which are connected with the epipubis are strictly comparable with those which are attached to the marsupial bones. But, in *Salamandra*, there is a muscle (Plate 8 [Plate 25], fig. 13, *A.*), of which I have been able to find no representative in the

Monotremes I have dissected. This is a thin band of longitudinal fibres, which spring partly from the pubis, close to the symphysis, and partly from the outer edge of the pedicle of the epipubis, and are inserted into the outer edge of the ramus (Plate 8 [Plate 25], fig. 13, *A.*). External to this, a broad flat band of muscular fibres (fig. 13, *B.*) takes its origin from the pubis and its pectineal process, and runs forwards to be inserted into the modified branchial arches and the tongue. These are the *hebosteoglossi* of von Siebold (" Observationes quædam de Salamandris et Tritonibus "). Superficial to this muscle, is the proper rectus (*R.*) itself, marked by its tendinous intersections; while, on the dorsal or deep side of both, there is a curious fan-shaped muscle (*C.*), which takes its origin from the pectineal process, by a narrow tendon, and spreads out to be inserted into the outer face of the pedicle and the outer edge of the ramus of its side. The ventral face of the pedicle and the posterior halves of the rami are closely adherent to the fascia of the external oblique in the middle line, and lie between the inner edges of the two recti. Finally, the fibres of the transversus (fig. 13, *Trs.*) are inserted into the outer edges of the rami, and the fascia which unites these appears to belong to the transversus.

On comparing the recti and the muscles A, B, C, with those of *Ornithorhynchus* and *Echidna*, a great apparent difference manifests itself. For the very thin recti of the Monotremes take their origin from the pubis along a line which extends from the tubercle to close to the symphysis, and pass forwards, dorsad of the marsupial bones and the pyramidales, which thus lie altogether in front of them and are, by them, largely separated from the fascia transversalis. Nevertheless, it will be observed that the origin of the muscle B nearly corresponds with that of the rectus in *Ornithorhynchus*; and I am disposed to think that, in this animal, the rectus, at least in its posterior moiety, is represented by the homologue of this muscle, which has extended laterally over the dorsal face of the enormously enlarged homologues of the rami of the ypsiloid cartilage.

However this may be, it must be recollected that it is only the extreme ends of the rami which lie dorsad of the recti, and that, in the rest of its extent, the epipubis of *Salamandra* is firmly fixed to the fascia of the external oblique, which forms the front wall of the sheath of the rectus. The homology of the epipubis with the marsupial bones is determined by the essential identity of the relations of the two to the tendons of the external oblique muscles.

It seems to me that, in such a pelvis as that of *Salamandra*, we

have an adequate representation of the type from which all the different modifications which we find in the higher Vertebrata may have taken their origin.

In the lizards and the *Chelonia* the iliac and obturator axes have inclined forwards, and the epipubes have been reduced to such rudiments as have been described in chameleons and in some tortoises.[1]

In the crocodiles, with the same general pelvic characters, the cotyloid end of the pubis retains its imperfectly ossified condition, while the epipubes represent the vastly enlarged rami of the salamandrine epipubis.

In the *Ornithoscelida* and in birds, the ilia elongate, but it is the modification of the pubes and ischia which is the most characteristic feature of the pelvis, and the epipubis vanishes.

In the *Pterosauria* and in the Dicynodonts, the salamandarine non-development of an obturator fontanelle persists; and in the former, the sessile rami of the epipubis appear to be represented by the so-called marsupial bones.

Unless the like should prove to be the case in the Dicynodonts, it is in the Mammalia alone that the subsacral portion of the ilium elongates backwards, carrying with it the pubis and the ischium, between which a large rounded obturator fontanelle is developed.

These facts appear to me to point to the conclusion that the Mammalia have been connected with the Amphibia by some unknown "pro-mammalian" group, and not by any of the known forms of Sauropsida; and there is other evidence which tends in the same direction.

Thus, the Amphibia are the only air-breathing Vertebrata, which, like Mammals, have a dicondylian skull. It is only in them that the articular element of the mandibular arch remains cartilaginous; while the quadrate ossification is small, and the squamosal extends down over it to the osseous elements of the mandible; thus affording an easy transition to the mammalian condition of these parts.

The pectoral arch of the Monotremes is as much amphibian as it is sauropsidan; the carpus and the tarsus of all Sauropsida, except the *Chelonia*, are modified away from the Urodele type, while those of the Mammal are directly reducible to it; and it is perhaps worth notice, that the calcar of the frogs is, in some respects, comparable with the spur of the Monotremes.

[1] Hoffman, "Beiträge zur Kenntniss des Beckens der Amphibien und Reptilien," "Nied. Archiv für Zoologie," Bd. 3, p. 143, 1876.

Huxley.

Fig 3.

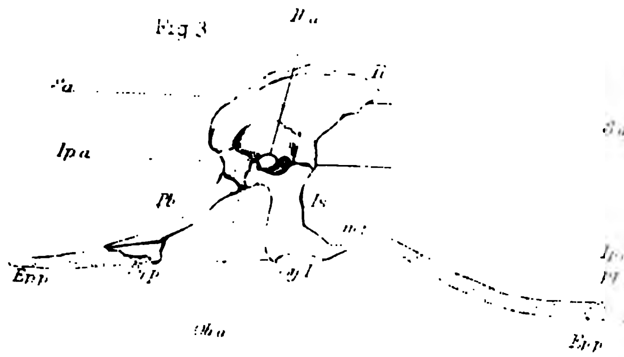


Fig 7.

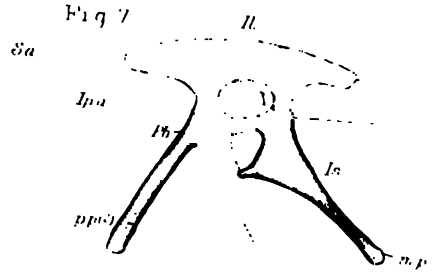


Fig 8

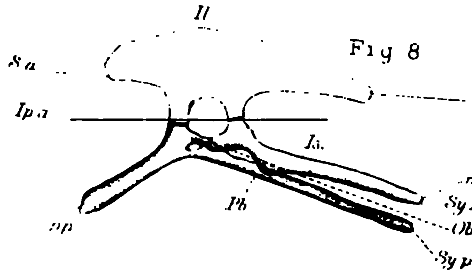


Fig. 9.

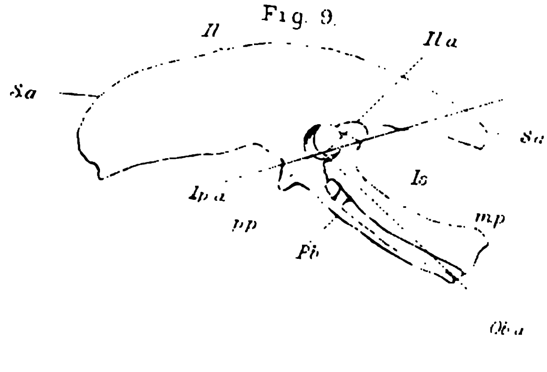
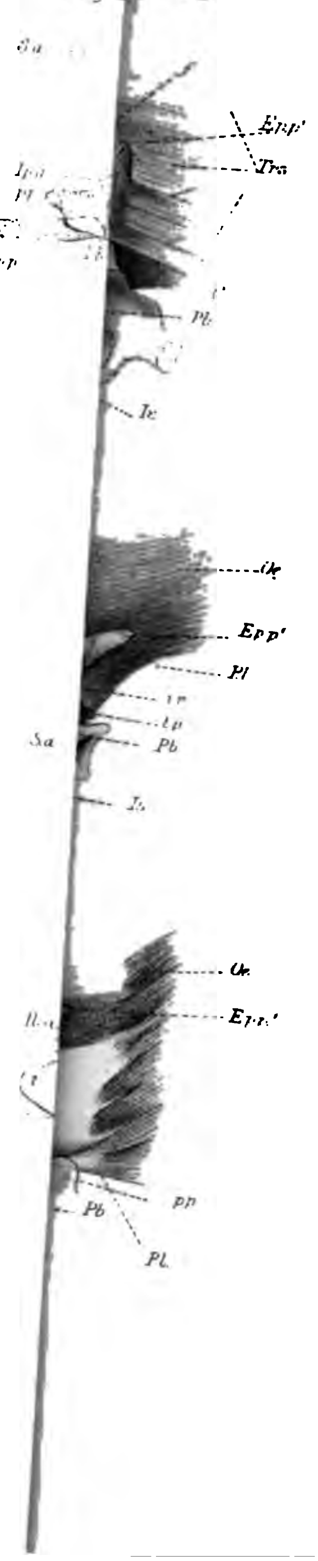


Fig. 13.



Finally, the fact that, in all Sauropsida, it is a right aortic arch which is the main conduit of arterial blood leaving the heart, while in Mammals, it is a left aortic arch which performs this office, is a great stumbling-block in the way of the derivation of the Mammalia from any of the Sauropsida. But, if we suppose the earliest forms of both the Mammalia and the Sauropsida to have had a common Amphibian origin, there is no difficulty in the supposition that, from the first, it was a left aortic arch in the one series, and the corresponding right aortic arch in the other, which became the predominant feeder of the arterial system.

The discovery of the intermediate links between Reptilia and Aves, among extinct forms of life, gives every ground for hoping that, before long, the transition between the lowest Mammalia at present known and the simpler Vertebrata may be similarly traced. The preceding remarks are intended to direct attention to the indications of the characters of these promammalian Vertebrata, which the evidence at present forthcoming seems to me to suggest.

In the relatively large size of the brain, and in the absence of teeth, the only existing representatives of the *Ornithodelphia* present characters which suggest that they are much modified members of the group. On comparing the brain of *Echidna*, for example, with that of many *Marsupialia* and *Insectivora*, its relative magnitude is remarkable: and, in view of the evidence which is now accumulating, that the brain increases in size in the later members of the same series of Mammalia, one may surmise that *Echidna* is the last term of a series of smaller-brained *Ornithodelphia*. Among the higher Vertebrata, I think that there is strong reason to believe that edentulous animals are always modifications of toothed forms.

EXPLANATION OF PLATE 8 [PLATE 25].

Figs. 1 to 9. The left half of the pubic arch in *Salamandra* (fig. 1), *Iguana* (fig. 2), *Crocodilus* (fig. 3), *Ornithorhynchus* (fig. 4), *Echidna* (fig. 5), *Lepus* (fig. 6), *Compsognathus* (fig. 7), *Laosaurus* (fig. 8), and *Apteryx* (fig. 9). The letters have the same signification throughout. *Il.* ilium, *Pb.* pubis, *Is.* ischium, *Ep. p.* epipubis, *S. a.* sacral axis, *Ip. a.* ilio-pectineal axis, *Ob. a.* obturator axis, *Il. a.* ilia axis, *Sy. p.*, *Sy. I.*, indicate the extent to which the pubes and the ischia unite respectively in their ventral symphyses; *p. p.* pectineal process, *t. p.* tuberosity or spine of the pubis, *m. p.* metischial process or tuberosity of the ischium, *Cl.* os cloacæ in *Iguana*.

Figs. 10, 11. Dorsal and ventral views of the ventral half of the pelvis of *Salamandra maculosa* (×4). The letters as before, except *Epp.*[1] *Epp.*[2], right and left rami of the epipubis or ypsiloid cartilage, *Ob. n.* foramen of the obturator nerve, *s.* trace of a suture between the ischium and the pubis, on the right side, *Ac.* acetabulum.

Fig. 12. Ventral aspect of the pelvis of a small *Crocodilus acutus* and the hindermost abdominal false ribs, of the natural size. The obturator nerve (*Ob. n.*) perforates the aponeurosis, which fills up the rhomboidal space between the ischia and the pubes, on the inner side of the pubis. *Sy. p. l.* the ligamentous union of the pubes.

Fig. 13. Dorsal aspect of the epipubis and the muscles connected with it in *Salamandra maculosa.* On the left side, the transversalis and the muscle *C.* are removed.

Fig. 15. The same, all the muscles but the external oblique being removed.

Fig. 14. The epipubis and the adjacent muscles in *Ornithorhynchus.*

R. rectus abdominus, *Py.* pyramidalis, *O. e.* obliquus externus, *Trs.* transversus, *l. a.* linea alba, *f.* fascia, extending between the two rami of the epipubis in *Salamandra*, *P.l.* the representative of Poupart's ligament, *i. r.* inguinal ring, *A. B. C.* muscles of Salamandra described in the text. *A*, and *C.* together appear to be the *pubio-marsupial* of Dugès : *B.* is the *hebosteoglossus* of von Siebold.

XX

ON SENSATION AND THE UNITY OF STRUCTURE OF SENSIFEROUS ORGANS

The Nineteenth Century, vol. v., April, 1879, *pp.* 597–611.

THE maxim that metaphysical inquiries are barren of result, and that the serious occupation of the mind with them is a mere waste of time and labour, finds much favour in the eyes of the many persons who pride themselves on the possession of sound common sense; and we sometimes hear it enunciated by weighty authorities, as if its natural consequence, the suppression of such studies, had the force of a moral obligation.

In this case, however, as in some others, those who lay down the law seem to forget that a wise legislator will consider, not merely whether his proposed enactment is desirable, but whether obedience to it is possible. For, if the latter question is answered negatively, the former is surely hardly worth debate.

Here, in fact, lies the pith of the reply to those who would make metaphysics contraband of intellect. Whether it is desirable to place a prohibitory duty upon philosophical speculations or not, it is utterly impossible to prevent the importation of them into the mind. And it is not a little curious to observe that those who most loudly profess to abstain from such commodities are all the while unconscious consumers, on a great scale, of one or other of their multitudinous disguises or adulterations. With mouths full of the particular kind of heavily buttered toast which they affect, they inveigh against the eating of plain bread. In truth, the attempt to nourish the human intellect upon a diet which contains no metaphysics is about as hopeful as that of certain Eastern sages to nourish their bodies without destroying life. Everybody has heard the story of the pitiless microscopist, who ruined the peace of mind

of one of these mild enthusiasts by showing him the animals moving in a drop of the water with which, in the innocency of his heart, he slaked his thirst ; and the unsuspecting devotee of plain common sense may look for as unexpected a shock when the magnifier of severe logic reveals the germs, if not the full-grown shapes, of lively metaphysical postulates rampant amidst his most positive and matter-of-fact notions.

By way of escape from the metaphysical Will-o'-the-wisps generated in the marshes of literature and theology, the serious student is sometimes bidden to betake himself to the solid ground of physical science. But the fish of immortal memory, who threw himself out of the frying-pan into the fire, was not more ill advised than the man who seeks sanctuary from philosophical persecution within the walls of the observatory or of the laboratory. It is said that "metaphysics" owe their name to the fact that, in Aristotle's works, questions of pure philosophy are dealt with immediately after those of physics. If so, the accident is happily symbolical of the essential relations of things ; for metaphysical speculation follows as closely upon physical theory as black care upon the horseman.

One need but mention such fundamental, and indeed indispensable, conceptions of the natural philosopher as those of atoms and forces : or that of attraction considered as action at a distance ; or that of potential energy ; or the antinomies of a vacuum and a plenum ; to call to mind the metaphysical background of physics and chemistry ; while, in the biological sciences, the case is still worse. What is an individual among the lower plants and animals? Are genera and species realities or abstractions? Is there such a thing as Vital Force? or does the name denote a mere relic of metaphysical fetichism? Is the doctrine of final causes legitimate or illegitimate? These are a few of the metaphysical topics which are suggested by the most elementary study of biological facts. But more than this, it may be truly said that the roots of every system of philosophy lie deep among the facts of physiology. No one can doubt that the organs and the functions of Sensation are as much a part of the province of the physiologist, as are the organs and functions of motion, or those of digestion ; and yet it is impossible to gain an acquaintance with even the rudiments of the physiology of sensation without being led straight to one of the most fundamental of all metaphysical problems. In fact the sensory operations have been from time immemorial the battle-ground of philosophers.

I have more than once taken occasion to point out that we are indebted to Descartes, who happened to be a physiologist as well

as a philosopher, for the first distinct enunciation of the essential elements of the true theory of sensation. In later times, it is not to the works of the philosophers, if Hartley and James Mill are excepted, but to those of the physiologists, that we must turn for an adequate account of the sensory process. Haller's luminous, though summary, account of sensation in his admirable *Primæ Lineæ*, the first edition of which was printed in 1747, offers a striking contrast to the prolixity and confusion of thought which pervade Reid's *Inquiry*, of seventeen years later date.[1] Even Sir William Hamilton, learned historian and acute critic as he was, not only failed to apprehend the philosophical bearing of long-established physiological truths; but, when he affirmed that there is no reason to deny that the mind feels at the finger points, and none to assert that the brain is the sole organ of thought,[2] he showed that he had not apprehended the significance of the revolution commenced, two hundred years before his time, by Descartes, and effectively followed up by Haller, Hartley, and Bonnet in the middle of the last century.

In truth, the theory of sensation, except in one point, is, at the present moment, very much where Hartley, led by a hint of Sir Isaac Newton's, left it, when, a hundred and twenty years since, the *Observations on Man: his Frame, his Duty, and his Expectations*, was laid before the world. The whole matter is put in a nutshell in the following passages of this notable book:—

"External objects impressed upon the senses occasion, first on the nerves on which they are impressed, and then on the brain, vibrations of the small and, as we may say, infinitesimal medullary particles.

[1] In justice to Reid, however, it should be stated that the chapters on Sensation in the *Essays on the Intellectual Powers* (1785) exhibit a great improvement. He is, in fact, in advance of his commentator, as the note to Essay II. chap. ii. p. 248 of Hamilton's edition shows.

[2] Haller, amplifying Descartes, writes in the *Primæ Lineæ*, CCCLXVI.—'Non est adeo obscurum sensum omnem oriri ab objecti sensibilis impressione in nervum quemcumque corporis humani, et eamdem per eum nervum ad cerebrum pervenientem tunc demum representari animæ, quando cerebrum adtigit. Ut etiam hoc falsum sit animam improximo per sensoria nervorumque ramos sentire.' . . . DLVII.—'Dum ergo sentimus quinque diversissima entia conjunguntur: corpus quod sentimus: organi sensorii adfectio ab eo corpore: cerebri adfectio a sensorii percussione nata: in anima nata mutatio: animæ denique conscientia et sensationis adperceptio.' Nevertheless, Sir William Hamilton gravely informs his hearers:—"We have no more right to deny that the mind feels at the finger points, as consciousness assures us, than to assert that it thinks exclusively in the brain."—*Lecture on Metaphysics and Logic*, ii. p. 128.—"We have no reason whatever to doubt the report of consciousness, that we actually perceive at the external point of sensation, and that we perceive the material reality."—*Ibid.* p. 129.

"These vibrations are motions backwards and forwards of the small particles; of the same kind with the oscillations of pendulums and the tremblings of the particles of sounding bodies. They must be conceived to be exceedingly short and small, so as not to have the least efficacy to disturb or move the whole bodies of the nerves or brain.[1]

"The white medullary substance of the brain is also the immediate instrument by which ideas are presented to the mind; or, in other words, whatever changes are made in this substance, corresponding changes are made in our ideas; and *vice versâ*."[2]

Hartley, like Haller, had no conception of the nature and functions of the grey matter of the brain. But, if for "white medullary substance," in the latter paragraph, we substitute "grey cellular substance," Hartley's propositions embody the most probable conclusions which are to be drawn from the latest investigations of physiologists. In order to judge how completely this is the case, it will be well to study some simple case of sensation, and following the example of Reid and of James Mill, we may begin with the sense of smell. Suppose that I become aware of a musky scent, to which the name of "muskiness" may be given. I call this an odour, and I class it along with the feelings of light, colours, sounds, tastes, and the like, among those phenomena which are known as sensations. To say that I am aware of this phenomenon, or that I have it, or that it exists, are simply different modes of affirming the same facts. If I am asked how I know that it exists, I can only reply that its existence and my knowledge of it are one and the same thing; in short, that my knowledge is immediate or intuitive, and, as such, is possessed of the highest conceivable degree of certainty.

The pure sensation of muskiness is almost sure to be followed by a mental state which is not a sensation, but a belief, that there is somewhere close at hand a something on which the existence of the sensation depends. It may be a musk-deer, or a musk-rat, or a musk-plant, or a grain of dry musk, or simply a scented handkerchief; but former experience leads us to believe that the sensation is due to the presence of one or other of these objects, and that it will vanish if the object is removed. In other words, there arises a belief in an external cause of the muskiness, which, in common language, is termed an odorous body.

[1] *Observations on Man*, vol. i. p. 11.

[2] *Ibid.* p. 8. The speculations of Bonnet are remarkably similar to those of Hartley; and they appear to have originated independently, though the *Essai de Psychologie* (1754) is of five years later date than the *Observations on Man* (1749).

But the manner in which this belief is usually put into words is strangely misleading. If we are dealing with a musk-plant, for example, we do not confine ourselves to a simple statement of that which we believe, and say that the musk-plant is the cause of the sensation called muskiness; but we say that the plant has a musky smell, and we speak of the odour as a quality, or property, inherent in the plant. And the inevitable reaction of words upon thought has in this case become so complete, and has penetrated so deeply, that when an accurate statement of the case—namely, that muskiness, inasmuch as the term denotes nothing but a sensation, is a mental state and has no existence except as a mental phenomenon —is first brought under the notice of common-sense folks, it is usually regarded by them as what they are pleased to call a mere metaphysical paradox and a patent example of useless subtlety. Yet the slightest reflection must suffice to convince any one possessed of sound reasoning faculties, that it is as absurd to suppose that muskiness is a quality inherent in one plant, as it would be to imagine that pain is a quality inherent in another, because we feel pain when a thorn pricks the finger.

Even the common-sense philosopher, *par excellence*, says of smell: "It appears to be a simple and original affection or feeling of the mind altogether inexplicable and unaccountable. It is indeed impossible that it can be in any body: it is a sensation, and a sensation can only be in a sentient thing." [1]

That which is true of muskiness is true of every other odour. Lavender-smell, clove-smell, garlic-smell, are, like "muskiness," names of states of consciousness, and have no existence except as such. But, in ordinary language, we speak of all these odours as if they were independent entities residing in lavender, cloves, and garlic; and it is not without a certain struggle that the false metaphysic of common sense, thus ingrained in us, is expelled.

It is unnecessary for the present purpose to inquire into the origin of our belief in external bodies, or into that of the notion of causation. Assuming the existence of an external world, there is no difficulty in obtaining experimental proof that, as a general rule, olfactory sensations are caused by odorous bodies; and we may pass

[1] *An Inquiry into the Human Mind on the Principles of Common Sense*, ch. ii. § 2. Reid affirms that "it is genius and not the want of it that adulterates philosophy, and fills it with error and false theory," and no doubt his own lucubrations are free from the smallest taint of the impurity to which he objects. But, for want of something more than that "common sense," which is very common and a little dull, the contemner of genius did not notice that the admission here made knocks so big a hole in the bottom of "common sense philosophy," that nothing can save it from foundering in the dreaded abyss of Idealism.

on to the next step of the inquiry—namely, how the odorous body produces the effect attributed to it.

The first point to be noted here is another fact revealed by experience; that the appearance of the sensation is governed, not only by the presence of the odorous substance, but by the condition of a certain part of our corporeal structure of the nose. If the nostrils are closed, the presence of the odorous substance does not give rise to the sensation; while, when they are open, the sensation is intensified by the approximation of the odorous substance to them, and by snuffing up the adjacent air in such a manner as to draw it into the nose. On the other hand, looking at an odorous substance, or rubbing it on the skin, or holding it to the ear, does not awaken the sensation. Thus, it can be readily established by experiment that the perviousness of the nasal passages is, in some way, essential to the sensory function; in fact, that the organ of that function is lodged somewhere in the nasal passages. And, since odorous bodies give rise to their effects at considerable distances, the suggestion is obvious that something must pass from them into the sense organ. What is this something which plays the part of an intermediary between the odorous body and the sensory organ?

The oldest speculation about the matter dates back to Democritus and the Epicurean School, and it is to be found fully stated in the fourth book of Lucretius. It comes to this: that the surfaces of bodies are constantly throwing off excessively attenuated films of their own substance; and that these films, reaching the mind, excite the appropriate sensations in it.

Aristotle did not admit the existence of any such material films, but conceived that it was the form of the substance, and not its matter, which affected sense, as a seal impresses wax, without losing anything in the process. While many, if not the majority, of the Schoolmen took up an intermediate position, and supposed that a something which was not exactly either material or immaterial, and which they called an "intentional species," effected the needful communication between the bodily cause of sensation and the mind.

But all these notions, whatever may be said for, or against, them in general, are fundamentally defective, by reason of an oversight which was inevitable, in the state of knowledge at the time in which they were promulgated. What the older philosophers did not know, and could not know, before the anatomist and physiologist had done his work, is that, between the external object and that mind in which they supposed the sensation to inhere, there lies a physical obstacle. The sense organ is not a mere passage by which the

"tenuia simulacra rerum," or the "intentional species" cast off by objects, or the "forms" of sensible things, pass straight to the mind; on the contrary, it stands as a firm and impervious barrier, through which no material particle of the world without can make its way to the world within.

Let us consider the olfactory sense organ more nearly. Each of the nostrils leads into a passage completely separated from the other by a partition, and these two passages place the nostrils in free communication with the back of the throat, so that they freely transmit the air passing to the lungs when the mouth is shut as in ordinary breathing. The floor of each passage is flat, but its roof is a high arch, the crown of which is seated between the orbital cavities of the skull, which serve for the lodgment and protection of the eyes; and therefore lies behind the apparent limits of that feature which in ordinary language is called the nose. From the side walls of the upper and back part of these arched chambers, certain delicate plates of bone project, and these, as well as a considerable part of the partition between the two chambers, are covered by a fine, soft, moist membrane. It is to this Schneiderian, or olfactory, membrane that odorous bodies must obtain direct access if they are to give rise to their appropriate sensations; and it is upon the relatively large surface which the olfactory membrane offers that we must seek for the seat of the organ of the olfactory sense. The only essential part of that organ consists of a multitude of minute rod-like bodies, set perpendicularly to the surface of the membrane, and forming a part of the cellular coat, or epithelium, which covers the olfactory membrane, as the epidermis covers the skin. In the case of the olfactory sense, there can be no doubt that the Democritic hypothesis, at any rate for such odorous substances as musk, has a good foundation. Infinitesimal particles of musk fly off from the surface of the odorous body, and, becoming diffused through the air, are carried into the nasal passages, and thence into the olfactory chambers, where they come into contact with the filamentous extremities of the delicate olfactory epithelium.

But this is not all. The "mind" is not, so to speak, upon the other side of the epithelium. On the contrary, the inner ends of the olfactory cells are connected with nerve fibres, and these nerve fibres, passing into the cavity of the skull, at length end in a part of the brain, the olfactory sensorium. It is certain that the integrity of each, and the physical inter-connection of all these three structures, the epithelium of the sensory organ, the nerve fibres, and the sensorium, are essential conditions of ordinary sensation. That is to

say, the air in the olfactory chambers may be charged with particles of musk; but, if either the epithelium, or the nerve fibres, or the sensorium are injured, or physically disconnected from one another, sensation will not arise. Moreover the epithelium may be said to be receptive, the nerve fibres transmissive, and the sensorium sensifacient. For, in the act of smelling, the particles of the odorous substance produce a molecular change (which Hartley was in all probability right in terming a vibration) in the epithelium, and this change, being transmitted to the nerve fibres, passes along them with a measurable velocity, and, finally reaching the sensorium, is immediately followed by the sensation.

Thus, modern investigation supplies a representative of the Epicurean simulacra in the volatile particles of the musk; but it also gives us the stamp of the particles on the olfactory epithelium, without any transmission of matter, as the equivalent of the Aristotelian "form"; while, finally, the modes of motion of the molecules of the olfactory cell, of the nerve, and of the cerebral sensorium, which are Hartley's vibrations, may stand very well for a double of the "intentional species" of the Schoolmen. And this last remark is not intended merely to suggest a fanciful parallel; for, if the cause of the sensation is, as analogy suggests, to be sought in the mode of motion of the object of sense, then it is quite possible that the particular mode of motion of the object is reproduced in the sensorium; exactly as the diaphragm of a telephone reproduces the mode of motion taken up at its receiving end. In other words, the secondary "intentional species" may be, as the Schoolmen thought the primary one was, the last link between matter and mind.

None the less, however, does it remain true that no similarity exists, nor indeed is conceivable, between the cause of the sensation and the sensation. Attend as closely to the sensations of muskiness, or any other odour, as we will, no trace of extension, resistance, or motion is discernible in them. They have no attribute in common with those which we ascribe to matter; they are, in the strictest sense of the words, immaterial entities.

Thus, the most elementary study of sensation justifies Descartes' position, that we know more of mind than we do of body; that the immaterial world is a firmer reality than the material. For the sensation "muskiness" is known immediately. So long as it persists, it is a part of what we call our thinking selves, and its existence lies beyond the possibility of doubt. The knowledge of an objective or material cause of the sensation, on the other hand, is mediate; it is a belief as contradistinguished from an intuition; and it is a belief

which, in any given instance of sensation, may, by possibility, be devoid of foundation. For odours, like other sensations, may arise from the occurrence of the appropriate molecular changes in the nerve or in the sensorium, by the operation of a cause distinct from the affection of the sense organ by an odorous body. Such "subjective" sensations are as real existences as any others and as distinctly suggest an external odorous object as their cause; but the belief thus generated is a delusion. And, if beliefs are properly termed "testimonies of consciousness," then undoubtedly the testimony of consciousness may be, and often is, untrustworthy.

Another very important consideration arises out of the facts as they are now known. That which, in the absence of a knowledge of the physiology of sensation, we call the cause of the smell, and term the odorous object, is only such, mediately, by reason of its emitting particles which give rise to a mode of motion in the sense organ. The sense organ, again, is only a mediate cause by reason of its producing a molecular change in the nerve fibre; while this last change is also only a mediate cause of sensation, depending, as it does, upon the change which it excites in the sensorium.

The sense organ, the nerve, and the sensorium, taken together, constitute the sensiferous apparatus. They make up the thickness of the wall between the mind, as represented by the sensation "muskiness," and the object, as represented by the particle of musk in contact with the olfactory epithelium.

It will be observed that the sensiferous wall and the external world are of the same nature; whatever it is that constitutes them both is expressible in terms of matter and motion. Whatever changes take place in the sensiferous apparatus are continuous with, and similar to, those which take place in the external world.[1] But

[1] The following diagrammatic scheme may help to elucidate the theory of sensation:—

Mediate Knowledge				Immediate Knowledge
	Sensiferous Apparatus			
Objects of Sense	Receptive (Sense Organ)	Transmissive (Nerve)	Sensificatory (Sensorium)	Sensations and other States of Consciousness
Hypothetical Substance of Matter				Hypothetical Substance of Mind
Physical World.				Mental World
Not Self	Self			
Non-Ego or Object				Ego or Subject

Immediate knowledge is confined to states of consciousness, or, in other words, to the

with the sensorium, matter and motion come to an end; while phenomena of another order, or immaterial states of consciousness, make their appearance. How is the relation between the material and the immaterial phenomena to be conceived? This is the metaphysical problem of problems, and the solutions which have been suggested have been made the corner-stones of systems of philosophy. Three mutually irreconcilable readings of the riddle have been offered.

The first is, that an immaterial substance of mind exists; and that it is affected by the mode of motion of the sensorium in such a way as to give rise to the sensation.

The second is, that the sensation is a direct effect of the mode of motion of the sensorium, brought about without the intervention of any substance of mind.

The third is, that the sensation is neither directly, nor indirectly, an effect of the mode of motion of the sensorium, but that it has an independent cause. Properly speaking, therefore, it is not an effect of the motion of the sensorium, but a concomitant of it.

As none of these hypotheses is capable of even an approximation to demonstration, it is almost needless to remark that they have been severally held with tenacity and advocated with passion. I do not think it can be said of any of the three that it is inconceivable, or that it can be assumed on *à priori* grounds to be impossible.

Consider the first, for example; an immaterial substance is perfectly conceivable. In fact, it is obvious that, if we possessed no sensations but those of smell and hearing, we should be unable to conceive a material substance. We might have a conception of time, but could have none of extension, or of resistance, or of motion. And without the three latter conceptions no idea of matter could be formed. Our whole knowledge would be limited to that of a shifting succession of immaterial phenomena. But, if an immaterial substance may exist, it may have any conceivable properties; and sensation may be one of them. All these propositions may be affirmed with complete dialectic safety, inasmuch as they cannot possibly be disproved; but neither can a particle of demonstrative evidence be offered in favour of them.

As regards the second hypothesis, it certainly is not inconceivable,

phenomena of mind. Knowledge of the physical world, or of one's own body and of objects external to it, is a system of beliefs or judgments based on the sensations. The term "self" is applied not only to the series of mental phenomena which constitute the ego, but to the fragment of the physical world which is their constant concomitant. The corporeal self, therefore, is part of the non-ego; and is objective in relation to the ego as subject.

and therefore it may be true, that sensation is the direct effect of certain kinds of bodily motion. It is just as easy to suppose this as to suppose, on the former hypothesis, that bodily motion affects an immaterial substance. But neither is it susceptible of proof.

And, as to the third hypothesis, since the logic of induction is in no case competent to prove that events apparently standing in the relation of cause and effect may not both be effects of a common cause—that also is as safe from refutation, if as incapable of demonstration, as the other two.

In my own opinion, neither of these speculations can be regarded seriously as anything but a more or less convenient working hypothesis. But, if I must choose among them, I take the "law of parcimony" for my guide, and select the simplest—namely, that the sensation is the direct effect of the mode of motion of the sensorium. It may justly be said that this is not the slightest explanation of sensation; but then am I really any the wiser if I say that a sensation is an activity (of which I know nothing) of a substance of mind (of which also I know nothing)? Or, if I say that the Deity causes the sensation to arise in my mind immediately after He has caused the particles of the sensorium to move in a certain way, is anything gained? In truth, a sensation, as we have already seen, is an intuition—a part of immediate knowledge. As such it is an ultimate fact and inexplicable; and all that we can hope to find out about it, and that indeed is worth finding out, is its relation to other natural facts. That relation appears to me to be sufficiently expressed, for all practical purposes, by saying that sensation is the invariable consequent of certain changes in the sensorium—or, in other words, that so far as we know, the change in the sensorium is the cause of the sensation.

I permit myself to imagine that the untutored, if noble, savage of common sense who has been misled into reading thus far by the hope of getting positive solid information about sensation, giving way to not unnatural irritation, may here interpellate: "The upshot of all this long disquisition is that we are profoundly ignorant. We knew that to begin with, and you have merely furnished another example of the emptiness and uselessness of metaphysics." But I venture to reply, Pardon me, you were ignorant, but you did not know it. On the contrary, you thought you knew a great deal, and were quite satisfied with the particularly absurd metaphysical notions which you were pleased to call the teachings of common sense. You thought that your sensations were properties of external things, and had an existence outside of yourself. You thought that you

knew more about material than you do about immaterial existences. And if, as a wise man has assured us, the knowledge of what we don't know is the next best thing to the knowledge of what we do know, this brief excursion into the province of philosophy has been highly profitable.

Of all the dangerous mental habits, that which schoolboys call "cocksureness" is probably the most perilous; and the inestimable value of metaphysical discipline is that it furnishes an effectual counterpoise to this evil proclivity. Whoso has mastered the elements of philosophy knows that the attribute of unquestionable certainty appertains only to the existence of a state of consciousness so long as it exists; all other beliefs are mere probabilities of a higher or lower order. Sound metaphysic is an amulet which renders its possessor proof alike against the poison of superstition and the counter-poison of nihilism; by showing that the affirmations of the former and the denials of the latter alike deal with matters about which, for lack of evidence, nothing can be either affirmed or denied.

I have dwelt at length upon the nature and origin of our sensations of smell, on account of the comparative freedom of the olfactory sense from the complications which are met with in most of the other senses.

Sensations of taste, however, are generated in almost as simple a fashion as those of smell. In this case, the sense organ is the epithelium which covers the tongue and the palate; and which sometimes, becoming modified, gives rise to peculiar organs termed "gustatory bulbs," in which the epithelial cells elongate and assume a somewhat rod-like form. Nerve fibres connect the sensory organ with the sensorium, and tastes or flavours are states of consciousness caused by the change of molecular state of the latter. In the case of the sense of touch there is often no sense organ distinct from the general epidermis. But many fishes and amphibia exhibit local modifications of the epidermic cells which are sometimes extraordinarily like the gustatory bulbs; more commonly, both in lower and higher animals, the effect of the contact of external bodies is intensified by the development of hair-like filaments, or of true hairs, the bases of which are in immediate relation with the ends of the sensory nerves. Every one must have noticed the extreme delicacy of the sensations produced by the contact of bodies with the ends of the hairs of the head; and the "whiskers" of cats owe their functional importance to the abundant supply of nerves to the follicles in which

their bases are lodged. What part, if any, the so-called "tactile corpuscles," "end bulbs," and "Pacinian bodies" play in the mechanism of touch is unknown. If they are sense organs, they are exceptional in character, in so far as they do not appear to be modifications of the epidermis. Nothing is known respecting the sense organs of those sensations of resistance which are grouped under the head of the muscular sense; nor of the sensations of warmth and cold; nor of that very singular sensation which we call tickling.

In the case of heat and cold, the organism not only becomes affected by external bodies, far more remote than those which affect the sense of smell; but the Democritic hypothesis is obviously no longer permissible. When the direct rays of the sun fall upon the skin, the sensation of heat is certainly not caused by "attenuated films" thrown off from that luminary, but to a mode of motion which is transmitted to us. In Aristotelian phrase, it is the form without the matter of the sun which stamps the sense organ; and this, translated into modern language, means nearly the same thing as Hartley's vibrations. Thus we are prepared for what happens in the case of the auditory and the visual senses. For neither the ear nor the eye receives anything but the impulses or vibrations originated by sonorous or luminous bodies. Nevertheless, the receptive apparatus still consists of nothing but specially modified epithelial cells. In the labyrinth of the ear of the higher animals the free ends of these cells terminate in excessively delicate hair-like filaments; while, in the lower forms of the auditory organ, its free surface is beset with delicate hairs like those of the surface of the body, and the transmissive nerves are connected with the bases of these hairs. Thus there is an insensible gradation in the forms of the receptive apparatus, from the organ of touch, on the one hand, to those of taste and smell; and, on the other hand, to that of hearing. Even in the case of the most refined of all the sense organs, that of vision, the receptive apparatus departs but little from the general type. The only essential constituent of the visual sense organ is the retina, which forms so small a part of the eyes of the higher animals; and the simplest eyes are nothing but portions of the integument, in which the cells of the epidermis have become converted into glassy rod-like retinal corpuscles. The outer ends of these are turned towards the light; their sides are more or less extensively coated with a dark pigment, and their inner ends are connected with the transmissive nerve fibres. The light impinging on these visual rods produces a change in them which is communicated to the nerve fibres, and,

being transmitted to the sensorium, gives rise to the sensation—if indeed all animals which possess eyes are endowed with what we understand as sensation.

In the higher animals, a complicated apparatus of lenses, arranged on the principle of a camera obscura, serves at once to concentrate and to individualise the pencils of light proceeding from external bodies. But the essential part of the organ of vision is still a layer of cells which have the form of rods with truncated or conical ends. By what seems a strange anomaly, however, the glassy ends of these are turned not towards, but away from, the light; and the latter has to traverse the layer of nervous tissues with which their outer ends are connected, before it can affect them. Moreover, the rods and cones of the vertebrate retina are so deeply seated, and in many respects so peculiar in character, that it appears impossible, at first sight, that they can have anything to do with that epidermis of which gustatory and tactile, and at any rate the lower forms of auditory and visual, organs are obvious modifications.

Whatever be the apparent diversities among the sensiferous apparatuses, however, they share certain common characters. Each consists of a receptive, a transmissive, and a sensificatory portion. The essential part of the first is an epithelium, of the second, nerve fibres, of the third, a part of the brain; the sensation is always the consequence of the mode of motion excited in the receptive, and sent along the transmissive, to the sensorial part of the sensiferous apparatus. And, in all the senses, there is no likeness whatever between the object of sense, which is matter in motion, and the sensation, which is an immaterial phenomenon.

On the hypothesis which appears to me to be the most convenient, sensation is a product of the sensiferous apparatus caused by certain modes of motion which are set up in it by impulses from without. The sensiferous apparatuses are, as it were, factories, all of which at the one end receive raw materials of a similar kind—namely, modes of motion—while, at the other, each turns out a special product, the feeling which constitutes the kind of sensation characteristic of it.

Or, to make use of a closer comparison, each sensiferous apparatus is comparable to a musical-box wound up; with as many tunes as there are separate sensations. The object of a simple sensation is the agent which presses down the stop of one of these tunes, and the more feeble the agent, the more delicate must be the mobility of the stop.[1]

[1] "Chaque fibre est une espèce de touche ou de marteau destiné à rendre un certain ton."—Bonnet, *Essai de Psychologie*, chap. iv.

But, if this be the case, if the recipient part of the sensiferous apparatus is, in all cases, merely a mechanism affected by coarser or finer kinds of material motion, we might expect to find that all sense organs are fundamentally alike, and result from the modification of the same morphological elements. And this is exactly what does result from all recent histological and embryological investigations.

It has been seen that the receptive part of the olfactory apparatus is a slightly modified epithelium, which lines an olfactory chamber deeply seated between the orbits in adult human beings. But, if we trace back the nasal chambers to their origin in the embryo, we find that, to begin with, they are mere depressions of the skin of the fore part of the head, lined by a continuation of the general epidermis. These depressions become pits, and the pits, by the growth of the adjacent parts, gradually acquire the position which they finally occupy. The olfactory organ, therefore, is a specially modified part of the general integument.

The human ear would seem to present greater difficulties. For the essential part of the sense organ, in this case, is the membranous labyrinth, a bag of complicated form, which lies buried in the depths of the floor of the skull, and is surrounded by dense and solid bone. Here, however, recourse to the study of development readily unravels the mystery. Shortly after the time when the olfactory organ appears as a depression of the skin on the side of the fore part of the head, the auditory organ appears as a similar depression on the side of its back part. The depression, rapidly deepening, becomes a small pouch, and then, the communication with the exterior becoming shut off, the pouch is converted into a closed bag, the epithelial lining of which is a part of the general epidermis segregated from the rest. The adjacent tissues, changing first into cartilage and then into bone, enclose the auditory sac in a strong case, in which it undergoes its further metamorphoses ; while the drum, the ear bones, and the external ear are superadded by no less extraordinary modifications of the adjacent parts. Still more marvellous is the history of the development of the organ of vision. In the place of the eye, as in that of the nose and that of the ear, the young embryo presents a depression of the general integument ; but in man and the higher animals, this does not give rise to the proper sensory organ, but only to part of the accessory structures concerned in vision. In fact, this depression, deepening and becoming converted into a shut sac, produces only the cornea, the aqueous humour, and the crystalline lens of the perfect eye.

The retina is added to this by the outgrowth of the wall of a

portion of the brain into a sort of bag or sac with a narrow neck, the convex bottom of which is turned outwards or towards the crystalline lens. As the development of the eye proceeds, the convex bottom of the bag becomes pushed in, so that it gradually obliterates the cavity of the sac, the previously convex wall of which becomes deeply concave. The sac of the brain is now like a double nightcap ready for the head, but the place which the head would occupy is taken by the vitreous humour, while the layer of nightcap next it becomes the retina. The cells of this layer which lie furthest from the vitreous humour, or, in other words, bound the original cavity of the sac, are metamorphosed into the rods and cones. Suppose now that the sac of the brain could be brought back to its original form ; then the rods and cones would form part of the lining of a side pouch of the brain. But one of the most wonderful revelations of embryology is the proof of the fact that the brain itself is, at its first beginning, merely an infolding of the epidermic layer of the general integument. Hence it follows that the rods and cones of the vertebrate eye are modified epidermic cells, as much as the crystalline cones of the insect or crustacean eye are; and that the inversion of the position of the former in relation to light arises simply from the roundabout way in which the vertebrate retina is developed.

Thus all the higher sense organs start from one foundation, and the receptive epithelium of the eye, or of the ear, is as much modified epidermis as is that of the nose. The structural unity of the sense organs is the morphological parallel to their identity of physiological function, which, as we have seen, is to be impressed by certain modes of motion ; and they are fine or coarse in proportion to the delicacy or the strength of the impulses by which they are to be affected.

In ultimate analysis, then, it appears that a sensation is the equivalent in terms of consciousness for a mode of motion of the matter of the sensorium. But, if inquiry is pushed a stage further, and the question is asked, What then do we know about matter and motion? there is but one reply possible. All that we know about motion is that it is a name for certain changes in the relations of our visual, tactile, and muscular sensations ; and all that we know about matter is that it is the hypothetical substance of physical phenomena—the assumption of the existence of which is as pure a piece of metaphysical speculation as that of the substance of mind.

Our sensations, our pleasures, our pains, and the relations of these make up the sum total of the elements of positive, unquestionable

knowledge. We call a large section of these sensations and their relations matter and motion ; the rest we term mind and thinking; and experience shows that there is a certain constant order of succession between some of the former and some of the latter.

This is all that just metaphysical criticism leaves of the idols set up by the spurious metaphysics of vulgar common sense. It is consistent either with pure Materialism, or with pure Idealism, but it is neither. For the Idealist, not content with declaring the truth that our knowledge is limited to facts of consciousness, affirms the wholly unprovable proposition that nothing exists beyond these and the substance of mind. And, on the other hand, the Materialist, holding by the truth that, for anything that appears to the contrary, material phenomena are the causes of mental phenomena, asserts his unprovable dogma, that material phenomena and the substance of matter are the sole primary existences.

Strike out the propositions about which neither controversialist does or can know anything, and there is nothing left for them to quarrel about. Make a desert of the Unknowable, and the divine Astræa of philosophic peace will commence her blessed reign.

XXI

THE PRESIDENT'S ADDRESS

The Journal of the Quekett Microscopical Club, vol. v., 1878–9, *pp.* 250–255.
(*Delivered at the Annual General Meeting, July 25th*, 1879.)

IN coming before you this evening, I should be glad if you will not consider the few observations which I am about to make, as representing anything so formal or serious as an Address, partly because an Address, in the ordinary sense of the term, is hardly so suited to the character of a Club as something of a more conversational character; and partly from personal reasons,—for it happens that owing to the undoubtedly fresh and open, but rather severe winter through which we are at present passing, I find myself with very little voice this evening, and fear that I shall have still less by the time I conclude.

Since I have held the honourable position of President of the Club, my attendance at your meetings has impressed me very strongly with the great amount of instrumental perfection which is to be observed on those occasions; and I do not think that any one could fail to be struck with the skill displayed in such work, nor could he fail to admire the great patience, the perseverance, the devotion of time and energy displayed by the members of the Club in the pursuit of microscopy.

No doubt one might say that a very large result of this activity is simple amusement; but I happen to be one of those people—perhaps because I get so little of it myself—who think that amusement is an exceedingly good thing; and I am strongly disposed to think the beneficial effects of such amusements as do no harm to a man himself, nor in any way rob his neighbour—especially such as are found in microscopical studies, heightened by the sympathy of those who are associated for the purpose—are very great, and that

they are much to be cherished as an important part of the good of human life. So that if it happened that no member pursued the subject for a higher purpose than the gratification of his taste for the beautiful, or the exercise of manipulative skill, I, for one, should think the time of the Club exceedingly well spent. But happily no one, whatever be his object, who works at the business of the Club, can end in simple amusement. He is dealing with natural objects, and every new thing observed, every fresh beauty discovered, is something added to the stock of natural knowledge; and every improvement of his instrument makes it a better weapon of scientific research. And not only so, but the habit of mind which creates the possibility of finding amusement in pursuits of this kind, is invaluable as a preparation for the reception of scientific truth, and the cultivation of scientific methods. If I may say so without offence, such amusement may be regarded as an involuntary ploughing and harrowing of the ground, making it receptive of the seeds of science, and preparing it for rich harvests in the future. So, as I said before, whatever member of the Club has joined it for the sake of mere amusement, has done a good thing for himself, and has done probably more than he knows to help those who make these pursuits the serious business of their lives.

But whilst recognising the legitimacy of following out such pursuits for amusement only, I have a sort of feeling in regard to them such as an old recruiting sergeant might be supposed to have whilst looking at a band of rustics sporting on a village green, or at a number of volunteers going through their evolutions. These athletic exercises and this playing at soldiers are all very well in their way; but the recruiting sergeant with an eye for a man, will see that the sport is training those who have a vocation for the realities of war, and is leaving them to feel their way towards taking part in more serious business. Many of the papers which I have heard in this room have given me the feeling that I should much like to give the shilling, and putting my hand upon the readers to say, "Your proper business is to come into the army of science." And naturally I must feel great gratitude to a society like this, as one of the army of workers who looks at it with an eye to enlistment.

I must, however, separate myself from the recruiting sergeant, because he walks off with his recruit, who is seen no more in the place that once knew him; while I cannot say positively, that those of you who have a turn for really scientific work may not do better to stop where you are. In fact, you have opportunities which are not possessed by the men who make science a business. The truth

is that the increase of knowledge has its drawbacks, not perhaps as Solomon said—"He that increaseth knowledge increaseth sorrow;" but certainly it is an increase of trouble and an increase of worry. Whoever becomes a man of science by profession must know something pretty thoroughly, and this means that he must not only know pretty accurately this or that piece of detailed work; he must have not only the knowledge of general facts, but must possess the special knowledge also, and be able to guide the one by the other, and to criticise his speculations by his knowledge of detail—this is the only title by which he can sustain his claim. But during the last quarter of a century science has taken to grow in a most portentous and astonishing fashion. I remember the time when it was quite easy for an ordinarily industrious man to keep up with the scientific literature of the period; if he made himself acquainted with what went on here, and if he read a French or German work now and then, it was enough; but, at the present day, to keep up with all that goes on, he must be a most industrious man indeed, and if he even tries to keep up with it he must do an amount of reading which is singularly demoralising to his habits of thought. If he wishes to work out any scientific points with accuracy and detail, it must be a very small matter which does not occupy him for months, and need his closest attention, during which time he will be drifting altogether away from the stream of progress of scientific knowledge. This constitutes the difficulty—*experto crede*—the great difficulty of being broad without being shallow, and of being deep without being narrow. Any one who has exceptional qualities of work or method may perhaps be able to keep creditably abreast with the course of progress, and to do some work of his own besides; but if he is not so gifted, he has before him one or other of these two unsatisfactory alternatives.

But you, members of this Club, are in this respect vastly better off, because you can give your attention to any one point which you want to get at the bottom of, and you are not likely to be pulled up by some student in the lecture room who has read the latest thing published, and who expresses surprise that you do not know all about it too. Consequently you can give your attention to your own subject as exclusively as you may desire. I do not mean to say that you do not lose anything, for naturally where you have to deal with the deeper problems you will never come to any good unless you have those principles to guide you; but, for three-fourths of the problems of microscopy, although you will require neatness and skill, clearness of eye, and lightness of hand for cutting and preparing

sections, the great amount of general knowledge which a man of science is required to have is of no consequence at all.

Several amongst your number have asked me to indicate those courses of inquiry which may best be commended to members of such a society as this, and it strikes me that the suggestion which I have just made supplies the answer. It is exactly in that field—the following up of details, tracing out minutiæ of structure, in occupying themselves with such questions as are only to be solved by long and patient devotion of time and dexterity, and a thorough knowledge of instrumental manipulation—it is exactly there that men of science find their difficulties, because the amount of time consumed is so great. Take, for example, the application of persistent watching to the unravelment of the life history of a vast number of low organisms; that is a process which has been adopted in respect to certain fungi in order to ascertain whether they are parasites or variations. In such a case the plan pursued is that of taking the spores and watching them step by step, and there is no other way of doing it; it involves enormous expenditure of time and great instrumental dexterity, but those who can follow it obtain results which are to be attained in no other way. The work of Mr. Dallinger and Dr. Drysdale, for instance, affords us a very remarkable example of this kind of observation: these two gentlemen mounted guard alternately over a microscope for days and days, watched one identical monad through all its stages; and they succeeded in tracing out its entire life history, and made an epoch in our knowledge of these lowest forms. Now suppose this kind of observation was to be directed to the *Infusoria* in general, what an opportunity there is for some of you! Why, there is not a single genus or species of which we may say that we know the whole history. The common *Paramecium*, for instance, is one of the commonest things that exists, yet nobody certainly knows whether it has any other mode of reproduction except by fission. The skill which I have seen displayed here is of immense value in such kind of work, and if only applied to it must very soon bring some good results. The like is true also of the *Acinetæ*; we know something about them, but nothing like a complete history; and it is a perfect opprobrium to science that nobody knows what an *Amœba* is. I do not mean to say that we do not know the things we call by that name when we see them, but that we are unable to say with certainty what are their modes of reproduction, what are their various states, which are vegetable and which are animal. Turn to the study of development, the whole of which is in a progressive state. We are

now carrying it so far that we can trace back a single group of organs to a particular portion of the dividing yolk mass, and the ultimate result will probably be to trace out each group of organs to the blastomeres from which it has proceeded. Thirty years ago if any one had talked of making sections of a butterfly's or a crayfish's embryo, it would have been regarded as something inconceivable; but now careful section makers will deal with these things in such a way as to be able to make you twenty sections through one of them. But as every one knows, this kind of thing cannot be followed out without a great expenditure of time and an amount of dexterity which it is not given to every one to attain.

Let me also point out that it is not necessary to go far a-field to find subjects for this kind of work; probably what is most wanted is an exhaustive study of some of the commonest things about us. The development of Rotifers, for example; why, these are the commonest things in the world. Kowalewsky, years ago, made a number of observations upon the common earth worm; let us see if in his conclusions he was right or wrong. It is not very difficult to make sections of these things, and it would be of great importance to get his observations confirmed. I have no doubt as to their correctness myself, but it would be very satisfactory to have them verified. I might turn to half-a-dozen kinds of similar observations with regard to the development of insects—say the presence of an amnion in some and not in others; any one who could make minute sections would solve the problem for us. It happens that some time ago I occupied myself with a very common subject, by way of carrying out my own precept of trying to get to the bottom of something. I had various reasons for doing this with the common crayfish, and I may say that the result has been very instructive; I mention it to show how much it is worth while to take up common things, if only to find out points about them which have been overlooked. The first thing I did was to examine the branchiæ, and in so doing I found to my surprise that there were two little filaments, about $\frac{1}{20}$ of an inch long, attached to the sides of the body. I had never seen any notice of these things, but I found by-and-by that Brandt and Ratzeburg had seen them. The curious thing about them was, that these two little filaments occupied the same position as gills, and from this I had little reason to doubt that they were rudimentary gills, and that there had been gills in that position at some time. I then thought if I could obtain some less modified forms of crayfish, such as are found still in Australia, I should be able to throw some light on the matter. I did so, and found in the

place of these rudiments perfectly developed branchiæ. This led me to seek for similarities of structure in the lobster and the marine crayfish, and these again led me on to examine other *Crustacea*; and I need hardly say that the bearing of all this upon the theory of evolution from a common type was very important. From these things I was led to look into the structure of the muscles, the spermatozoa, the chitinous cuticle, the eye, and other parts, and there was not one of these which did not present interesting novelties and would not have taken months of work to get to the bottom of it, so as to make oneself thoroughly acquainted with every detail. You may find plenty of work if even you confine yourselves to such common things as caterpillars. Lyonet, you know, spent many years over his caterpillar, and the result was a monograph which will last for all time.

This is the kind of service which those members of the Club may perform who feel inclined for it; it is work which may be of very great value, and which certainly cannot be undertaken by those who have to occupy themselves with science as a whole.

I think that this is the pith of the remarks which I wished to offer to you this evening, and I find for the reasons already mentioned that I am coming to the end of my tether; but if you will take them as hints and suggestions, they will I am sure receive amplification as you seek to act upon them.

It remains now for me only to do two things—first I have to express my regret for the inefficient manner in which I have performed the not very onerous duties of President of the Club—but I think I may remind you that at the commencement of the term, I ventured to prophesy that such was likely to be the case; the reason, however, has certainly not been the lack of any interest in your proceedings, but simply that I am one of those working men of science whose labours are somewhat manifold; and in the second place, I have to thank you for the kindness and courtesy with which I have been received on this and on all other occasions, and to congratulate you on the election of your next President, who will, I hope, make up to you for all the deficiencies of your present retiring President.

XXII

ON CERTAIN ERRORS RESPECTING THE STRUCTURE OF THE HEART ATTRIBUTED TO ARISTOTLE

Nature, vol. xxi., November 6th, 1879, *pp.* 1–5.

IN all the commentaries upon the "Historia Animalium" which I have met with, Aristotle's express and repeated statement, that the heart of man and the largest animals contains only three cavities, is noted as a remarkable error. Even Cuvier, who had a great advantage over most of the commentators in his familiarity with the subject of Aristotle's description, and whose habitual caution and moderation seem to desert him when the opportunity of panegyrising the philosopher presents itself, is betrayed into something like a sneer on this topic.

"Du reste il n'attribue à cet organe que trois cavités, erreur qui prouve au moins qu'il en avait regardé la structure."[1]

To which remark, what follows will, I think, justify the reply, that it "prouve au moins" that Cuvier had not given ordinary attention, to say nothing of the careful study which they deserve, to sundry passages in the first and the third books of the "Historia" which I proceed to lay before the reader.

For convenience of reference these passages are marked *a, b, c,* &c.[2]

(Book i. 17).—(*a*) "The heart has three cavities, it lies above the ung on the division of the windpipe, and has a fatty and thick membrane where it is united with the great vein and the aorta. It lies upon the aorta, with its point down the chest, in all animals that have a chest. In all, alike in those that have a chest and in those

[1] "Histoire des Sciences Naturelles," i. p. 152.

[2] The text I have followed is that given by Aubert and Wimmer, "Aristoteles Thierkunde; kritsich berichtigter Text mit deutschen Uebersetzung;" but I have tried here and there to bring the English version rather closer to the original than the German translation, excellent as it is, seems to me to be.

that have none, the foremost part of it is the apex. This is often overlooked through the turning upside down of the dissection. The rounded end of the heart is uppermost, the pointed end of it is largely fleshy and thick, and in its cavities there are tendons. In other animals which have a chest the heart lies in the middle of the chest; in men, more to the left side, between the nipples, a little inclined to the left nipple in the upper part of the chest. The heart is not large, and its general form is not elongated but rounded, except that the apex is produced into a point.

(*b*) "It has, as already stated, three cavities, the largest of them is on the right, the smallest on the left, the middle-sized one in the middle; they have all, also the two small ones, passages (*τετρημένας*) towards the lung, very evidently as respects one of the cavities. In the region of the union [with the great vein and the aorta] the largest cavity is connected with the largest vein (near which is the mesentery); the middle cavity, with the aorta.

(*c*) "Canals (*πόροι*) from the heart pass to the lung and divide in the same fashion as the windpipe does, closely accompanying those from the windpipe through the whole lung. The canals from the heart are uppermost.

(*d*) "No canal is common [to the branches of the windpipe and those of the vein] (*οὐδεὶς δ'ἐστὶ κοινὸς πόρος*) but through those parts of them which are in contact (*τὴν σύναψιν*) the air passes in and they [the *πόροι*] carry it to the heart.

(*e*) "One of the canals leads to the right cavity, the other to the left.

(*f*) "Of all the viscera, the heart alone contains blood [in itself]. The lung contains blood, not in itself but in the veins, the heart in itself; for in each of the cavities there is blood; the thinnest is in the middle cavity."

(Book iii. 3).—(*g*) "Two veins lie in the thorax alongside the spine, on its inner face; the larger more forwards, the smaller behind; the larger more to the right, the smaller, which some call *aorta* (on account of the tendinous part of it seen in dead bodies), to the left. These take their origin from the heart; they pass entire, preserving the nature of veins, through the other viscera that they reach; while the heart is rather a part of them, and more especially of the anterior and larger one, which is continued into veins above and below, while between these is the heart.

(*h*) "All hearts contain cavities, but in those of very small animals the largest (cavity) is hardly visible, those of middling size have another, and the biggest all three.

(*i*) "The point of the heart is directed forwards, as was mentioned at first; the largest cavity to the right and upper side of it, the smallest to the left, and the middle-sized one between these; both of these are much smaller than the largest.

(*k*) "They are all connected by passages (συντέτρηνται) with the lung, but on account of the smallness of the canals this is obscure except in one.

(*l*) "The great vein proceeds from the largest cavity which lies upwards and to the right; next through the hollow middle (διὰ τοῦ κοίλου τοῦ μέσου) it becomes vein again, this cavity being a part of the vein in which the blood stagnates.

(*m*) "The aorta [proceeds from] the middle [cavity], but not in the same way, for it is connected [with the middle cavity] by a much more narrow tube (σύριγγα).

(*n*) "The [great] vein extends through the heart, towards the aorta from the heart.

(*o*) "The great vein is membranous like skin, the aorta narrower than it and very tendinous, and as it extends towards the head and the lower parts it becomes narrow and altogether tendinous.

(*p*) "In the first place, a part of the great vein extends upwards from the heart towards the lung and the attachment of the aorta, the vein being large and undivided. It divides into two parts, the one to the lung, the other to the spine and the lowest vertebra of the neck.

(*q*) "The vein which extends to the lung first divides into two parts for the two halves of it and then extends alongside each tube (σύριγγα) and each passage (τρῆμα), the larger beside the larger and the smaller beside the smaller, so that no part [of the lung] can be found from which a passage (τρῆμα) and a vein are absent. The terminations are invisible on account of their minuteness, but the whole lung appears full of blood. The canals from the vein lie above the tubes given off from the windpipe."

The key to the whole of the foregoing description of the heart lies in the passages (*g*) and (*l*). They prove that Aristotle, like Galen, five hundred years afterwards, and like the great majority of the old Greek anatomists, did not reckon what we call the right auricle as a constituent of the heart at all, but as a hollow part or dilatation of the "great vein." Aristotle is careful to state that his observations were conducted on suffocated animals; and if any one will lay open the thorax of a dog or a rabbit, which has been killed with chloroform, in such a manner as to avoid wounding any important vessel, he will at once see why Aristotle adopted this view.

For, the vena cava inferior (*b*), the right auricle (*R.a*) and the vena

cava superior and innominate vein (*V.I*) distended with blood, seem to form one continuous column, to which the heart is attached as a sort of appendage (*g*). This column is, as Aristotle says, vein above (*a*) and vein below (*b*), the upper and the lower divisions being connected *διὰ τοῦ κοῖλου τοῦ μέσου*—or by means of the intervening cavity or chamber (*R.a*)—which is the right auricle.

But when, from the four cavities of the heart recognised by us moderns, one is excluded, there remain three—which is just what Aristotle says. The solution of the difficulty is, in fact, as absurdly simple as that presented by the egg of Columbus ; and any error there may be is not to be put down to Aristotle, but to that inability to comprehend that the same facts may be accurately described in different ways, which is the special characteristic of the commentatorial mind. That the three cavities mentioned by Aristotle are just those which remain if the right auricle is omitted, is plain enough from what is said in (*b*), (*c*), (*e*), (*i*), and (*l*). For, in a suffocated animal, the "right cavity" which is directly connected with the great vein and is obviously the right ventricle, being distended with blood, will look much larger than the middle cavity, which, since it gives rise to the aorta, can only be the left ventricle. And this, again, will appear larger than the thin and collapsed left auricle, which must be Aristotle's left cavity, inasmuch as this cavity is said to be connected by *πόροι* with the lung. The reason why Aristotle considered the left auricle to be a part of the heart, while he merged the right auricle in the great vein, is, obviously, the small relative size of the venous trunks and their sharper demarcation from the auricle. Galen, however, perhaps more consistently, regarded the left auricle also as a mere part of the "arteria venosa." The canal which leads from the right cavity of the heart to the lung is, without doubt, the pulmonary artery. But it may be said that, in this case, Aristotle contradicts himself, inasmuch as in (*p*) and (*q*) a vessel which is obviously the pulmonary artery, is described as a branch of the great vein. However, this difficulty also disappears if we reflect that, in Aristotle's way of looking at the matter, the line of demarcation between the great vein and the heart coincides with the right auriculo-ventricular aperture ; and that, inasmuch as the conical prolongation of the right ventricle which leads to the pulmonary artery (Fig. 1 *R.v'*), lies close in front of the auricle, its base may very easily (as the figure shows) be regarded as part of the general opening of the great vein into the right ventricle. In fact, it is clear that Aristotle, having failed to notice the valves of the heart, did not distinguish the part of the right ventricle from which the pulmonary artery arises (*R.v'*) from

the proper trunk of the artery on the one hand, and from the right auricle (*R.a*) on the other. Thus the root, as we may call it, of the pulmonary artery and the right auricle, taken together, are spoken of as the "part of the great vein which extends upwards;" and, as the

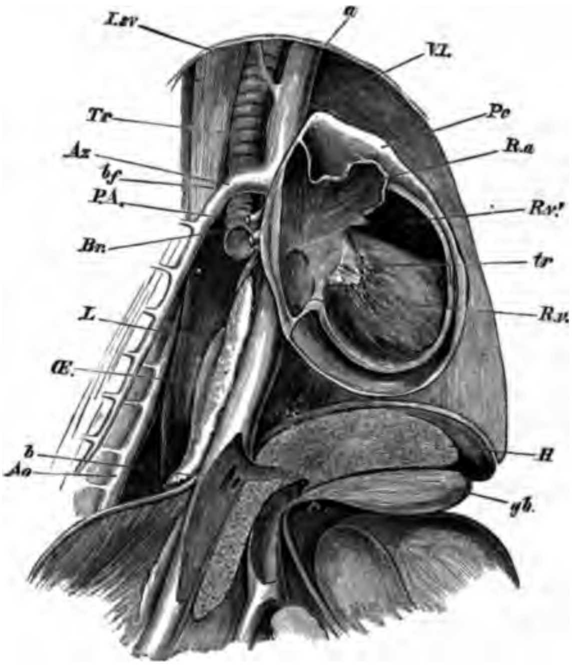


FIG. 1.—A dog having been killed by chloroform, enough of the right wall of the thorax was removed, without any notable bleeding, to expose the thoracic viscera. A carefully measured outline sketch of the parts *in situ* was then made, and on dissection, twenty-four hours afterwards, the necessary anatomical details were added. The woodcut is a faithfully reduced copy of the drawing thus constructed; and it represents the relations of the heart and great vessels as Aristotle saw them in a suffocated animal.

All but the inner lobe of the right lung has been removed: as well as the right half of the pericardium and the right walls of the right auricle and ventricle. It must be remembered that the thin transparent pericardial membrane appears nothing like so distinct in nature.

a,*b*., Aristotle's "great vein"; *V.I*, right vena innominata and vena cava superior; *b*, the inferior vena cava; *R.a*, the "hollow middle" part of the great vein or the right auricle; *R.v'*, the prolongation of the cavity of the right ventricle *R.v* towards the pulmonary artery; *tr*, one of the tricuspid valves; *Pc*, the pericardium; *I.sv*, superior intercortal vein; *Az*, vena azygos; *P.A.*, right pulmonary artery; *Br*, right bronchus; *L*, posterior lobe of the right lung; *Œ*, œsophagus; *Ao*, descending aorta; *H*, liver, in section, with hepatic vein, vena portæ, and gall-bladder, *gb*, separated by the diaphragm, also seen in section, from the thoracic cavity.

vena azygos (*Az*) was one branch of this, so the "vein to the lung" was another branch of it. But the latter branch, being given off close to the connection of the great vein with the ventricle, was also counted as one of the two πόροι by which the "heart" (that is to say

the right ventricle, the left ventricle, and the left auricle of our nomenclature) communicates with the lung.

The only other difficulty that I observe is connected with (*k*). If Aristotle intended by this to affirm that the middle cavity (left ventricle), like the other two, is directly connected with the lung by a *πόρος*, he would be in error. But he has excluded this interpretation of his words by (*e*), in which the number and relations of the canals, the existence of which he admits, are distinctly defined. I can only imagine then, that so far as this passage applies to the left ventricle, it merely refers to the indirect communication of that cavity with the vessels of the lungs, through the left auricle.

On this evidence I submit that there is no escape from the conclusion that, instead of having committed a gross blunder, Aristotle has given a description of the heart which, so far as it goes, is remarkably accurate. He is in error only in regard to the differences which he imagines to exist between large and small hearts (*h*).

Cuvier (who has been followed by other commentators) ascribes another error to Aristotle :—

"Aristote suppose que la trachée-artère se prolonge jusqu'au cœur, et semble croire, en conséquence, que l'air y pénètre (*l. c.* p. 152)."

Upon what foundation Cuvier rested the first of these two assertions, I am at a loss to divine. As a matter of fact, it will appear from the following excerpts that Aristotle gives an account of the structure of the lungs which is almost as good as that of the heart, and that it contains nothing about any prolongation of the windpipe to the heart.

"Within the neck lie what is called the œsophagus (so named on account of its length and its narrowness) and the windpipe (*ἀρτηρία*). The position of the windpipe in all animals that have one, is in front of the œsophagus. All animals which possess a lung have a windpipe. The windpipe is of a cartilaginous nature and is exsanguine, but is surrounded by many little veins . . . .

"It goes downwards towards the middle of the lung and then divides for each of the halves of the lung. In all animals that possess one, the lung is divided into two parts; but, in those which bring forth their young alive, the separation is not equally well marked, least of all in man.

"In oviparous animals, such as birds, and in quadrupeds which are oviparous, the one half of the lung is widely separated from the other; so that it appears as if they had two lungs. And from being single the windpipe becomes [divided into] two, which extend to each

half of the lung. It is fastened to the great vein and to what is called the aorta. When the windpipe is blown up the air passes into the hollow parts of the lung. In these, are cartilaginous tubes (*διαφύσεις*) which unite at an angle; from the tubes passages (*τρήματα*) traverse the whole of the lung; they are continually given off, the smaller from the larger." (Book i., 16.)

That Aristotle speaks of the lung as a single organ divided into two halves and says that the division is least marked in man, is puzzling at first, but becomes intelligible if we reflect upon the close union of the bronchi, the pulmonary vessels and the mediastinal walls of the pleuræ in mammals;[1] and it is quite true that the lungs are much more obviously distinct from one another in birds.

Aubert and Wimmer translate the last paragraph of the passage just cited as follows:—

"Diese haben aber knorpelige Scheidewände, welche unter spitzen Winkeln zusammentreten, und aus ihnen führen Oeffnungen durch die ganze Lunge, in dem sie sich in immer kleineren verzweigen."

But I cannot think that by *διαφύσεις* and *τρήματα*, in this passage, Aristotle meant either "partitions" or openings in the ordinary sense of the latter word. For, in Book iii., cap. 3, in describing the distribution of the "vein which goes to the lung" (the pulmonary artery), he says that it

"Extends alongside each tube (*σύριγγα*) and each passage (*τρῆμα*), the larger beside the larger, and the smaller beside the smaller; so that no part [of the lung] can be found from which a passage (*τρῆμα*) and a vein are absent."

Moreover, in Book i., 17, he says—

"Canals (*πόροι*) from the heart pass to the lung and divide in the same fashion as the windpipe does, closely accompanying those from the windpipe through the whole lung."

And again in Book i., 17—

"It (the lung) is entirely spongy, and alongside of each tube (*σύριγγα*) run canals (*πόροι*) from the great vein."

On comparing the last three statements with the facts of the case, it is plain that by *σύριγγες*, or tubes, Aristotle means the bronchi and so many of their larger divisions as obviously contain cartilages; and that by *διαφύσεις χονδρώδεις* he denotes the same things; and, if this be so, then the *τρήματα* must be the smaller bronchial canals, in which the cartilages disappear.

[1] In modern works on Veterinary Anatomy the lungs are sometimes described as two lobes of a single organ.

This view of the structure of the lung is perfectly correct so far as it extends; and, bearing it in mind, we shall be in a position to understand what Aristotle thought about the passage of air from the lungs into the heart. In every part of the lung, he says, in effect, there is an air tube which is derived from the trachea, and other tubes which are derived from the πόροι which lead from the lung to the heart, *suprà* (*c*). Their applied walls constitute the thin "synapses" (τὴν σύναψιν) through which the air passes out of the air tubes into the πόροι, or blood vessels, by transudation or diffusion; for there is no community between the cavities of the air tubes and cavities of the canals; that is to say, no opening from one into the other, *suprà* (*d*).

"On the words "κοινὸς πόρος" Aubert and Wimmer remark (*l. c.* p. 239), "Da A. die Ansicht hat die Lungenluft würde dem Herzen zugeführt, so postulirt er statt vieler kleiner Verbindungen einen grossen Verbindungsgang zwischen Lunge und Herz."

But does Aristotle make this assumption? The only evidence so far as I know in favour of the affirmative answer to this question is the following passage:—

"Συνήρτεται δὲ καὶ ἡ καρδία τῇ ἀρτηρίᾳ πιμελώδεσι καὶ χονδρώδεσι καὶ ἰνώδεσι δεσμοῖς· ᾗ δέ συνήρτεται, κοῖλόν ἐστιν. φυσωμένης δὲ τῆς ἀρτηρίας ἐν ἐνίοις μὲν οὐ κατάδηλον ποιεῖ, ἐν δὲ τοῖς μείζοσι τῶν ζώων δῆλον ὅτι εἰσέρχεται τὸ πνεῦμα εἰς αὐτήν" (i. cap. 16).

"The heart and the windpipe are connected by fatty and cartilaginous and fibrous bands; where they are connected it is hollow. Blowing into the windpipe does not show clearly in some animals, but in the larger animals it is clear that the air goes into it."

Aubert and Wimmer give a somewhat different rendering of this passage:—

"Auch das Herz hängt mit der Luftröhre durch fettreiche, knorpelige und faserige Bänder zusammen; und da, wo sie zusammenhängen, ist eine Höhlung. Beim Aufblasen der Lunge wird es bei manchen Thieren nicht wahrnehmbar, bei den grösseren aber ist es offenbar, dass die Luft in das Herz gelangt."

The sense here turns upon the signification which is to be ascribed to εἰς αὐτήν. But if these words refer to the heart, then Aristotle has distinctly pointed out the road which the air, in his opinion, takes namely, through the "synapses"; and there is no reason that I can discover to believe that he "postulated" any other and more direct communication.

With respect to the meaning of *κοῖλόν ἐστιν*, Aubert and Wimmer observe:—

"Dies scheint wohl die kurze Lungenvene zu sein. Schneider bezieht dies auf die Vorkammern, allein diese werden unten als Höhlen des Herzens beschrieben."

I am disposed to think, on the contrary, that the words refer simply to the cavity of the pericardium. For a part of this cavity (*sinus transversus pericardii*) lies between the aorta, on the one hand, and the pulmonary vessels with the bifurcation of the trachea, on the other hand, and is much more conspicuous in some animals than in man. It is strictly correct, therefore, in Aristotle's words, to say that where the heart and the windpipe are connected "it is hollow." If he had meant to speak of one of the pulmonary veins, or of any of the cavities of the heart, he would have used the terms *πόροι* or *κοιλίας* which he always employs for these parts.

According to Aristotle, then, the air taken into the lungs passes from the final ramifications of the bronchial tubes into the corresponding branches of the pulmonary blood vessels, not through openings, but by transudation, or, as we should nowadays say, diffusion, through the thin partitions formed by the applied coats of the two sets of canals. But the "pneuma" which thus reached the interior of the blood vessels was not, in Aristotle's opinion, exactly the same thing as the air. It was "*ἀήρ πολὺς ῥέων καὶ ἀθρόος*" ("De Mundo," iv., 9)—subtilized and condensed air; and it is hard to make out whether Aristotle considered it to possess the physical properties of a gas or those of a liquid. As he affirms that all the cavities of the heart contain blood (*f*), it is clear that he did not hold the erroneous view propounded in the next generation by Erasistratus. On the other hand, the fact that he supposes that the spermatic arteries do not contain blood but only an *αἱματώδης ὑγρόν* ("Hist. Animalium," iii., 1), shows that his notions respecting the contents of the arteries were vague. Nor does he seem to have known that the pulse is characteristic only of the arteries; and as he thought that the arteries end in solid fibrous bands, he naturally could not have entertained the faintest conception of the true motion of the blood. But without attempting to read into Aristotle modern conceptions which never entered his mind, it is only just to observe that his view of what becomes of the air taken into the lungs is by no means worthy of contempt as a gross error. On the contrary, here, as in the case of his anatomy, what Aristotle asserts is true as far as it goes. Something does actually pass from the air contained in the lungs through the coats of the vessels into the blood, and thence to the

heart; to wit, oxygen. And I think that it speaks very well for ancient Greek science that the investigator of so difficult a physiological problem as that of respiration, should have arrived at a conclusion, the statement of which after the lapse of more than two thousand years, can be acceped as a thoroughly established scientific truth.

I trust that the case in favour of removing the statements about the heart from the list of the "errors of Aristotle" is now clear; and that the evidence proves, on the contrary, that they justify us in forming a very favourable estimate of the oldest anatomical investigations among the Greeks of which any sufficient record remains.

But is Aristotle to be credited with the merit of having ascertained so much of the truth? This question will not appear superfluous to those who are acquainted with the extraordinary history of Aristotle's works, or who adopt the conclusion of Aubert and Wimmer, that, of the ten books of the "Historia Animalium" which have come down to us, three are largely or entirely spurious and that the others contain many interpolations by later writers.

It so happens, however, that, apart from other reasons, there are satisfactory internal grounds for ascribing the account of the heart to a writer of the time at which Aristotle lived. For, within thirty years of his death, the anatomists of the Alexandrian school had thoroughly investigated the structure and the functions of the valves of the heart. During this time, the manuscripts of Aristotle were in the possession of Theophrastus; and no interpolater of later date would have shown that he was ignorant of the nature and significance of these important structures, by the brief and obscure allusion—"in its cavities there are tendons (*a*)." On the other hand, Polybus, whose account of the vascular system is quoted in the "Historia Animalium," was an elder contemporary of Aristotle. Hence, if any part of the work faithfully represents that which Aristotle taught, we may safely conclude that the description of the heart does so. Having granted this much, however, it is another question, whether Aristotle is to be regarded as the first discoverer of the facts which he has so well stated, or whether he, like other men, was the intellectual child of his time and simply carried on a step or two the work which had been commenced by others.

On the subject of Aristotle's significance as an original worker in biology extraordinarily divergent views have been put forward. If we are to adopt Cuvier's estimate, Aristotle was simply a miracle:—

"Avant Aristote la philosophie, entièrement spéculative, se

perdait dans les abstractions dépourvues de fondement ; la science n'existait pas. Il semble qu'elle soit sortie toute faite du cerveau d'Aristote comme Minerve, toute armée, du cerveau de Jupiter. Seul, en effet, sans antécédents, sans rien emprunter aux siècles qui l'avaient précédé, puisqu'ils n'avaient rien produit de solide, le disciple de Platon découvrit et démontra plus de vérités, executa plus de travaux scientifiques en un vie de soixante-deux ans, qu'après lui vingt siècles n'en ont pu faire,"[1] &c., &c.

" Aristote est le premier qui ait introduit la méthode de l'induction, de la comparaison des observations pour en faire sortir des idées générales, et celle de l'expérience pour multiplier les faits dont ces idées générales peuvent être déduites."—ii. p. 515.

The late Mr. G. H. Lewes,[2] on the contrary, tells us "on a superficial examination, therefore, he [Aristotle] will seem to have given tolerable descriptions; especially if approached with that disposition to discover marvels which unconsciously determines us in our study of eminent writers. But a more unbiased and impartial criticism will disclose that he has given no single anatomical description of the least value. All that he knew may have been known, and probably was known, without dissection. . . . . I do not assert that he never opened an animal ; on the contrary, it seems highly probable that he had opened many . . . . . . He never followed the course of a vessel or a nerve ; never laid bare the origin and insertion of a muscle ; never discriminated the component parts of organs ; never made clear to himself the connection of organs into systems."--(pp. 156–7).

In the face of the description of the heart and lungs, just quoted, I think we may venture to say that no one who has acquired even an elementary practical acquaintance with anatomy, and knows of his own knowledge that which Aristotle describes, will agree with the opinion expressed by Mr. Lewes ; and those who turn to the accounts of the structure of the rock lobster and that of the lobster, or to that of the Cephalopods and other Mollusks, in the fourth book of the " Historia Animalium," will probably feel inclined to object to it still more strongly.

On the other hand, Cuvier's exaggerated panegyric will as little bear the test of cool discussion. In Greece, the century before Aristotle's birth was a period of great intellectual activity, in the field of physical science no less than elsewhere. The method of induction

[1] " Histoire des Sciences Naturelles."—t. i. p. 130.

[2] " Aristotle, a Chapter from the History of Science."

has never been used to better effect than by Hippocrates; and the labours of such men as Alkmeon, Demokritus, and Polybus among Aristotle's predecessors, Diokles, and Praxagoras, among his contemporaries, laid a solid foundation for the scientific study of anatomy and development, independently of his labours. Aristotle himself informs us that the dissection of animals was commonly practised; that the aorta had been distinguished from the great vein; and that the connection of both with the heart had been observed by his predecessors. What they thought about the structure of the heart itself, or that of the lungs, he does not tell us, and we have no means of knowing. So far from arrogantly suggesting that he owed nothing to his predecessors, Aristotle is careful to refer to their observations and to explain why, in his judgment, they fell into the errors which he corrects.

Aristotle's knowledge, in fact, appears to have stood in the same relation to that of such men as Polybus and Diogenes of Apollonia, as that of Herophilus and Erasistratus did to his own, so far as the heart is concerned. He carried science a step beyond the point at which he found it; a meritorious, but not a miraculous, achievement. What he did required the possession of very good powers of observation; if they had been powers of the highest class he could hardly have left such conspicuous objects as the valves of the heart to be discovered by his successors.

And this leads me to make a final remark upon a singular feature of the "Historia Animalium." As a whole, it is a most notable production, full of accurate information and of extremely acute generalisations of the observations accumulated by naturalists up to that time. And yet, every here and there, one stumbles upon assertions respecting matters which lie within the scope of the commonest inspection, which are not so much to be called errors as stupidities. What is to be made of the statement that the sutures of women's skulls are different from those of men; that men and sundry male animals have more teeth than their respective females; that the back of the skull is empty, and so on? It is simply incredible to me that the Aristotle who wrote the account of the heart, also committed himself to absurdities which can be excused by no theoretical prepossession and which are contradicted by the plainest observation.

What, after all, were the original manuscripts of the "Historia Animalium"? If they were notes of Aristotle's lectures taken by some of his students, any lecturer who has chanced to look through

such notes would find the interspersion of a foundation of general and sometimes minute accuracy, with patches of transcendent blundering, perfectly intelligible. Some competent Greek scholar may perhaps think it worth while to tell us what may be said for or against the hypothesis thus hinted. One obvious difficulty in the way of adopting it is the fact that, in other works, Aristotle refers to the "Historia Animalium" as if it had already been made public by himself.

XXIII

ON THE EPIPUBIS IN THE DOG AND FOX.

Proceedings of the Royal Society of London, vol. xxx., 1879-1880, *pp.* 162, 163.
(*Read February 5th*, 1880.)

IN 1871[1] I gave a brief description of a structure which I had observed in the dog, in the following terms:—

"In the myology of the dog, the insertion of the tendon of the external oblique muscle of the abdomen presents some interesting peculiarities. The outer and posterior fibres of this muscle end in a fascia, which is partly continued over the thigh as *fascia lata*, and partly forms an arch (Poupart's ligament) over the femoral vessels; by its inner end it is inserted into the outer side of a triangular fibro-cartilage, the broad base of which is attached to the anterior margin of the pubis, between its spine and the symphysis, while its apex lies in the abdominal parietes. The internal tendon of the external oblique unites with the tendon of the internal oblique to form the inner pillar of the abdominal ring, and is inserted into the inner side of the triangular fibro-cartilage. The *pectineus* is attached to the ventral face of the cartilage; the outer part of the tendon of the rectus into its dorsal face; but the chief part of that tendon is inserted into the pubis behind it. This fibro-cartilage appears to represent the marsupial bone, or cartilage, of the Monotremes and Marsupials."

The only reference to this statement which I have met with is by Professor Macalister, in his "Introduction to the Systematic Zoology and the Morphology of Vertebrate Animals" (1878), p. 265:—

"Professor Huxley describes a fibro-cartilaginous 'marsupial' above the pubis, from whose anterior surface the pectineus arises. I have failed to satisfy myself of its existence as a constant structure in many dogs, in the common and Bengal foxes, in the dingo, jackal, *Canis pallipes*, and wolf."

The wording of this passage does not make it quite clear whether

[1] "Manual of the Anatomy of Vertebrated Animals," p. 417.

the writer has not found the structure in any case, but does not mean to deny that it may occur occasionally in the various *Canidæ* he mentions; or whether he has found it occasionally, but not constantly, in all or some of them.

Under these circumstances, it may be desirable to publish the fact that, having recently dissected, for purposes of comparison, a male and female fox and a male and female dog, I have not had the slightest difficulty in demonstrating the existence of the structure which I described in 1871, in all four. And the only phrase which appears to require modification in that description is the use of the term fibro-cartilage. I do not remember whether, formerly, I submitted the structure to microscopic examination or not; but in the specimens lately examined, notwithstanding the firmness and density of the triangular plate, it contains no true cartilage cells, but is entirely composed of fibrous bands which lie parallel with one another in the middle of the plate, while, at the thickened edges, they become closely interwoven.

A comparison of this triangular fibrous plate in the fox, with the "marsupial" bones of *Phalangista vulpina*, shows that the fibrous plate in the former animal exactly answers to the basal part of the "marsupial" bone in the latter. It may properly, therefore, be termed the *epipubic ligament*, and must be regarded as a structure of the same order as the rudimentary clavicle and the rudimentary hallux of the *Canidæ*; that is to say, as the remains of an organ which was fully developed in the ancestral forms of that group.

It is interesting to remark, in connexion with this interpretation of the facts, that, in the existing *Thylacinus*, which presents so many curious points of resemblance to the dogs, the epipubis is not ossified. As, however, the *Canidæ* have certainly existed since the Eocene epoch, there is no likelihood of the existence of any direct genetic connexion between the dogs and the Thylacines. The existing carnivorous *Marsupialia* have evidently all proceeded from ancestral forms, characterised by the possession of a thumb-like hallux, a peculiarity which is presented neither by the dogs, when they possess a hallux, nor by any other Carnivora with pentadactyle hind feet. Moreover, the early birth of the young and the development of a marsupium in the female, are evidences of the departure of the existing Marsupialia from the direct line by which the Mammalia have advanced from the ornithodelphous type. That the ancestors of all mammals possessed bony or cartilaginous epipubes is, I think, highly probable, but it does not follow that they had the marsupial method of bearing and nourishing their young.

XXIV

THE COMING OF AGE OF THE ORIGIN OF SPECIES.

Nature, vol. xxii., 1880, *pp.* 1–4. (*A Lecture delivered at the Royal Institution, Friday, March* 19*th*, 1880.)

MANY of you will be familiar with the aspect of this small green-covered book. It is a copy of the first edition of the *Origin of Species*, and bears the date of its production—the first of October, 1859. Only a few months, therefore, are needed to complete the full tale of twenty-one years since its birthday.

Those whose memories carry them back to this time will remember that the infant was remarkably lively, and that a great number of excellent persons mistook its manifestations of a vigorous individuality for mere naughtiness; in fact there was a very pretty turmoil about its cradle. My recollections of the period are particularly vivid; for, having conceived a tender affection for a child of what appeared to me to be such remarkable promise, I acted for some time in the capacity of a sort of under-nurse, and thus came in for my share of the storms which threatened even the very life of the young creature. For some years it was undoubtedly warm work, but considering how exceedingly unpleasant the apparition of the new-comer must have been to those who did not fall in love with him at first sight, I think it is to the credit of our age that the war was not fiercer, and that the more bitter and unscrupulous forms of opposition died away as soon as they did.

I speak of this period as of something past and gone, possessing merely a historical, I had almost said an antiquarian interest. For, during the second decade of the existence of the *Origin of Species*, opposition, though by no means dead, assumed a different aspect. On the part of all those who had any reason to respect themselves, it

assumed a thoroughly respectful character. By this time the dullest began to perceive that the child was not likely to perish of any congenital weakness or infantile disorder, but was growing into a stalwart personage, upon whom mere goody scoldings and threatenings with the birch-rod were quite thrown away.

In fact, those who have watched the progress of science within the last ten years will bear me out to the full when I assert that there is no field of biological inquiry in which the influence of the *Origin of Species* is not traceable; the foremost men of science in every country are either avowed champions of its leading doctrines, or at any rate abstain from opposing them; a host of young and ardent investigators seek for and find inspiration and guidance in Mr. Darwin's great work; and the general doctrine of Evolution, to one side of which it gives expression, finds in the phenomena of biology a firm base of operations whence it may conduct its conquest of the whole realm of nature.

History warns us, however, that it is the customary fate of new truths to begin as heresies and to end as superstitions; and, as matters now stand, it is hardly rash to anticipate that, in another twenty years, the new generation, educated under the influences of the present day, will be in danger of accepting the main doctrines of the *Origin of Species* with as little reflection, and it may be with as little justification, as so many of our contemporaries, twenty years ago, rejected them.

Against any such a consummation let us all devoutly pray; for the scientific spirit is of more value than its products, and irrationally-held truths may be more harmful than reasoned errors. Now the essence of the scientific spirit is criticism. It tells us that to whatever doctrine claiming our assent we should reply, Take it if you can compel it. The struggle for existence holds as much in the intellectual as in the physical world. A theory is a species of thinking, and its right to exist is coextensive with its power of resisting extinction by its rivals.

From this point of view it appears to me that it would be but a poor way of celebrating the Coming of Age of the *Origin of Species* were I merely to dwell upon the facts, undoubted and remarkable as they are, of its far-reaching influence and of the great following of ardent disciples who are occupied in spreading and developing its doctrines. Mere insanities and inanities have before now swollen to portentous size in the course of twenty years. Let us rather ask this prodigious change in opinion to justify itself; let us inquire whether anything has happened since 1859 which will explain, on rational

grounds, why so many are worshipping that which they burned, and burning that which they worshipped. It is only in this way that we shall acquire the means of judging whether the movement we have witnessed is a mere eddy of fashion, or truly one with the irreversible current of intellectual progress, and, like it, safe from retrogressive reaction.

Every belief is the product of two factors: the first is the state of the mind to which the evidence in favour of that belief is presented; and the second is the logical cogency of the evidence itself. In both these respects the history of biological science during the last twenty years appears to me to afford an ample explanation of the change which has taken place; and a brief consideration of the salient events of that history will enable us to understand why, if the *Origin of Species* appeared now, it would meet with a very different reception from that which greeted it in 1859.

One-and-twenty years ago, in spite of the work commenced by Hutton and continued with rare skill and patience by Lyell, the dominant view of the past history of the earth was catastrophic. Great and sudden physical revolutions, wholesale creations and extinctions of living beings, were the ordinary machinery of the geological epic brought into fashion by the misapplied genius of Cuvier. It was gravely maintained and taught that the end of every geological epoch was signalised by a cataclysm, by which every living being on the globe was swept away, to be replaced by a brand-new creation when the world returned to quiescence. A scheme of nature which appeared to be modelled on the likeness of a succession of rubbers of whist, at the end of each of which the players upset the table and called for a new pack, did not seem to shock anybody.

I may be wrong, but I doubt if at the present time there is a single responsible representative of these opinions left. The progress of scientific geology has elevated the fundamental principle of uniformitarianism, that the explanation of the past is to be sought in the study of the present, into the position of an axiom; and the wild speculations of the catastrophists, to which we all listened with respect a quarter of a century ago, would hardly find a single patient hearer at the present day. No physical geologist now dreams of seeking outside the ranges of known natural causes for the explanation of anything that happened millions of years ago, any more than he would be guilty of the like absurdity in regard to current events.

The effect of this change of opinion upon biological speculation is obvious. For, if there have been no periodical general physical catastrophes, what brought about the assumed general extinctions

and re-creations of life which are the corresponding biological catastrophes? And if no such interruptions of the ordinary course of nature have taken place in the organic, any more than in the inorganic, world, what alternative is there to the admission of Evolution?

The doctrine of Evolution in Biology is the necessary result of the logical application of the principles of uniformitarianism to the phenomena of life. Darwin is the natural successor of Hutton and Lyell, and the *Origin of Species* the natural sequence of the *Principles of Geology*.

The fundamental doctrine of the *Origin of Species*, as of all forms of the theory of Evolution applied to biology, is "that the innumerable species, genera, and families of organic beings with which the world is peopled have all descended, each within its own class or group, from common parents, and have all been modified in the course of descent."[1]

And, in view of the facts of geology, it follows that all living animals and plants "are the lineal descendants of those which lived long before the Silurian epoch."[2]

It is an obvious consequence of this theory of Descent with Modification, as it is sometimes called, that all plants and animals, however different they may now be, must, at one time or other, have been connected by direct or indirect intermediate gradations, and that the appearance of isolation presented by various groups of organic beings must be unreal.

No part of Mr. Darwin's work ran more directly counter to the prepossessions of naturalists twenty years ago than this. And such prepossessions were very excusable, for there was undoubtedly a great deal to be said, at that time, in favour of the fixity of species and of the existence of great breaks, which there was no obvious or probable means of filling up, between various groups of organic beings.

For various reasons, scientific and unscientific, much had been made of the hiatus between man and the rest of the higher mammalia, and it is no wonder that issue was first joined on this part of the controversy. I have no wish to revive past and happily forgotten controversies, but I must state the simple fact that the distinctions in cerebral and other characters, which were so hotly affirmed to separate man from all other animals in 1860, have all been demonstrated to be non-existent, and that the contrary doctrine is now universally accepted and taught.

But there were other cases in which the wide structural gaps asserted to exist between one group of animals and another were by

[1] *Origin of Species*, ed. 1, p. 457.

[2] *Ibid.*, ed. 1, p. 458.

no means fictitious; and when such structural breaks were real, Mr. Darwin could account for them only by supposing that the intermediate forms which once existed had become extinct. In a remarkable passage he says:—

"We may thus account even for the distinctness of whole classes from each other—for instance of birds from all other vertebrate animals—by the belief that many animal forms of life have been utterly lost, through which the early progenitors of birds were formerly connected with the early progenitors of the other vertebrate classes."[1]

Adverse criticism made merry over such suggestions as these. Of course it was easy to get out of the difficulty by supposing extinction; but where was the slightest evidence that such intermediate forms between birds and reptiles as the hypothesis required ever existed? And then probably followed a tirade upon this terrible forsaking of the paths of "Baconian induction."

But the progress of knowledge has justified Mr. Darwin to an extent which could hardly have been anticipated. In 1862, the specimen of *Archæopteryx*, which until the last two or three years has remained unique, was discovered; and it is an animal which, in its feathers and the greater part of its organisation, is a veritable bird, while, in other parts, it is as distinctly reptilian.

In 1868, I had the honour of bringing under your notice, in this theatre, the results of investigations made, up to that time, into the anatomical characters of certain ancient reptiles, which showed the nature of the modifications in virtue of which the type of the quadrupedal reptile passed into that of the bipedal bird; and abundant confirmatory evidence of the justice of the conclusions which I then laid before you has since come to light.

In 1875, the discovery of the toothed birds of the cretaceous formation in North America, by Prof. Marsh, completed the series of transitional forms between birds and reptiles, and removed Mr. Darwin's proposition that "many animal forms of life have been utterly lost, through which the early progenitors of birds were formerly connected with the early progenitors of the other vertebrate classes," from the region of hypothesis to that of demonstrable fact.

In 1859, there appeared to be a very sharp and clear hiatus between vertebrated and invertebrated animals, not only in their structure, but, what was more important, in their development. I do not think that we even yet know the precise links of connection

[1] *Origin of Species*, ed. 1, p. 431.

between the two; but the investigations of Kowalewsky and others upon the development of *Amphioxus* and of the *Tunicata* prove beyond a doubt that the differences which were supposed to constitute a barrier between the two are non-existent. There is no longer any difficulty in understanding how the vertebrate type may have arisen from the invertebrate, though the full proof of the manner in which the transition was actually effected may still be lacking.

Again, in 1859, there appeared to be a no less sharp separation between the two great groups of flowering and flowerless plants. It is only subsequently that the series of remarkable investigations inaugurated by Hofmeister has brought to light the extraordinary and altogether unexpected modifications of the reproductive apparatus in the *Lycopodiaceæ*, the *Rhizocarpeæ*, and the *Gymnospermeæ*, by which the ferns and the mosses are gradually connected with the Phanerogamic division of the vegetable world.

So, again, it is only since 1859 that we have acquired that wealth of knowledge of the lowest forms of life which demonstrates the futility of any attempt to separate the lowest plants from the lowest animals, and shows that the two kingdoms of living nature have a common borderland which belongs to both or to neither.

Thus it will be observed that the whole tendency of biological investigations since 1859 has been in the direction of removing the difficulties which the apparent breaks in the series created at that time; and the recognition of gradation is the first step towards the acceptance of evolution.

As another great factor in bringing about the change of opinion which has taken place among naturalists, I count the astonishing progress which has been made in the study of embryology. Twenty years ago, not only were we devoid of any accurate knowledge of the mode of development of many groups of animals and plants, but the methods of investigation were rude and imperfect. At the present time there is no important group of organic beings the development of which has not been carefully studied, and the modern methods of hardening and section-making enable the embryologist to determine the nature of the process in each case, with a degree of minuteness and accuracy which is truly astonishing to those whose memories carry them back to the beginnings of modern histology. And the results of these embryological investigations are in complete harmony with the requirements of the doctrine of Evolution. The first beginnings of all the higher forms of animal life are similar, and however diverse their adult conditions, they start from a common foundation. Moreover the process of development of the animal or

the plant from its primary egg or germ is a true process of evolution —a progress from almost formless to more or less highly organised matter, in virtue of the properties inherent in that matter.

To those who are familiar with the process of development all *à priori* objections to the doctrine of biological evolution appear childish. Any one who has watched the gradual formation of a complicated animal from the protoplasmic mass which constitutes the essential element of a frog's or a hen's egg has had under his eyes sufficient evidence that a similar evolution of the animal world from the like foundation is, at any rate, possible.

Yet another product of investigation has largely contributed to the removal of the objections to the doctrine of Evolution current in 1859. It is the proof afforded by successive discoveries that Mr. Darwin did not over estimate the imperfection of the geological record. No more striking illustration of this is needed than a comparison of our knowledge of the mammalian fauna of the Tertiary epoch in 1859 with its present condition. M. Gaudry's researches on the fossils of Pikermi were published in 1868, those of Messrs. Leidy, Marsh, and Cope on the fossils of the Western Territories of America have appeared almost wholly since 1870; those of M. Filhol, on the phosphorites of Quercy, in 1878. The general effect of these investigations has been to introduce us to a multitude of extinct animals, the existence of which was previously hardly suspected; just as if zoologists were to become acquainted with a country, hitherto unknown, as rich in novel forms of life, as Brazil or South Africa once were to Europeans. Indeed the fossil fauna of the Western Territories of America bids fair to exceed in interest and importance all other known Tertiary deposits put together; and yet, with the exception of the case of the American tertiaries, these investigations have extended over very limited areas, and at Pikermi were confined to an extremely small space.

Such appear to me to be the chief events in the history of the progress of knowledge, during the last twenty years, which account for the changed feeling with which the doctrine of Evolution is at present regarded by those who have followed the advance of biological science in respect of those problems which bear indirectly upon that doctrine.

But all this remains mere secondary evidence. It may remove dissent, but it does not compel assent. Primary and direct evidence in favour of Evolution can be furnished only by palæontology. The geological record, so soon as it approaches completeness, must, when properly questioned, yield either an affirmative or a negative

answer; if evolution has taken place, there will its mark be left; if it has not taken place, there will lie its refutation.

What was the state of matters in 1859? Let us hear Mr. Darwin, who may be trusted always to state the case against himself as strongly as possible.

"On this doctrine of the extermination of an infinitude of connecting links between the living and extinct inhabitants of the world, and at each successive period between the extinct and still older species, why is not every geological formation charged with such links? Why does not every collection of fossil remains afford plain evidence of the gradation and mutation of the forms of life? We meet with no such evidence, and this is the most obvious and plausible of the many objections which may be urged against my theory."[1]

Nothing could have been more useful to the opposition than this characteristically candid avowal, twisted as it immediately was into an admission that the writer's views were contradicted by the facts of palæontology. But, in fact, Mr. Darwin made no such admission. What he says in effect is, not that palæontological evidence is against him, but that it is not distinctly in his favour; and without attempting to attenuate the fact, he accounts for it by the scantiness and the imperfection of that evidence.

What is the state of the case now, when, as we have seen, the amount of our knowledge respecting the mammalia of the Tertiary epoch is increased fifty-fold, and in some directions even approaches completeness?

Simply this, that if the doctrine of Evolution had not existed palæontologists must have invented it, so irresistibly is it forced upon the mind by the study of the remains of the Tertiary mammalia, which have been brought to light since 1859.

Among the fossils of Pikermi, Gaudry found the successive stages by which the ancient civets passed into the more modern hyænas; through the Tertiary deposits of Western America, Marsh tracked the successive forms by which the ancient stock of the horse has passed into its present form; and innumerable less complete indications of the mode of evolution of other groups of the higher mammalia have been obtained.

In the remarkable memoir on the Phosphorites of Quercy, to which I have referred, M. Filhol describes no fewer than seventeen varieties of the genus *Cynodictis*, which fill up all the interval between the viverine animals and the bear-like dog *Amphicyon*; nor do I

[1] *Origin of Species*, ed. 1, p. 463.

know any solid ground of objection to the supposition that in this *Cynodictis-Amphicyon* group we have the stock whence all the Viveridæ, Felidæ, Hyænidæ, Canidæ, and perhaps the Procyonidæ and Ursidæ, of the present fauna have been evolved. On the contrary, there is a great deal to be said in its favour.

In the course of summing up his results, M. Filhol observes [1]:—

"During the epoch of the phospherites, great changes took place in animal forms, and almost the same types as those which now exist became defined from one another.

"Under the influence of natural conditions of which we have no exact knowledge, though traces of them are discoverable, species have been modified in a thousand ways: races have arisen which, becoming fixed, have thus produced a corresponding number of secondary species."

In 1859, language of which this is an unintentional paraphrase, occurring in the *Origin of Species*, was scouted as wild speculation; at present, it is a sober statement of the conclusions to which an acute and critically-minded investigator is led by large and patient study of the facts of palæontology. I venture to repeat what I have said before, that, so far as the animal world is concerned, Evolution is no longer a speculation, but a statement of historical fact. It takes its place alongside of those accepted truths which must be taken into account by philosophers of all schools.

Thus when, on the first day of October next, the *Origin of Species* comes of age, the promise of its youth will be amply fulfilled; and we shall be prepared to congratulate the venerated author of the book, not only that the greatness of his achievement and its enduring influence upon the progress of knowledge have won him a place beside our Harvey; but, still more, that, like Harvey, he has lived long enough to outlast detraction and opposition, and to see the stone that the builders rejected become the head-stone of the corner.

[1] This passage was omitted in the delivery of the lecture.

XXV

ON THE CRANIAL AND DENTAL CHARACTERS OF THE CANIDÆ.

Proceedings of the Scientific Meetings of the Zoological Society of London for the year 1880, *pp.* 238–288. (*Read April 6th,* 1880.)

1. THE unsatisfactory character of the attempts which have hitherto been made to determine the natural affinities of the numerous members of the group of Canine Carnivores must have impressed itself upon the mind of every one who has paid close attention to these animals. But I do not think that the discussion of the merits and demerits of the various systems of classification of the Canidæ which have been proposed would serve any useful purpose; and it is the less incumbent upon me to undertake the task at present, as I propose to deal with the question in a manner somewhat different, so far as I know, from any which has yet been pursued.

The general uniformity of the structure of the Canidæ is well known. There is a remarkable constancy in the characters of all the

organs, down even to the minuter details of the patterns of the crowns of the teeth, accompanied by variations, within comparatively narrow limits, in the form and proportion of the parts. The number of the præsacral and sacral vertebræ always remains the same, and that of the caudal vertebræ varies only within narrow limits. In the skull, there is a considerable range in the proportions of the jaws to the brain-case, and in the extent to which the temporal ridges, always widely separate in young animals, approach and coalesce into a sagittal crest in the adult. The greater or less backward extension of the nasal bones, the union or separation of the nasal processes of the frontal bones with the ascending processes of the præmaxillaries, and the variations in the form of the supra-orbital processes have been noted. The straightness or angulation of the line of the molar and præmolar teeth, and the proportions of the sectorial teeth to those which follow them, have been taken into account, as well as minor characters of the teeth themselves. Attention has been directed to the excess of teeth above the normal number in *Otocyon*, and to the diminution of the number in *Cyon* and *Icticyon*. The variation in size of the pollex and its disappearance in *Lycaon* are well known. The differences in the form of the pupil have been noted; and, of late, particular notice has been taken of the extensive modifications in the form of the cæcum. Weight has been attached to the presence or absence of a caudal gland.

The taxonomic value of these variations, however, has remained doubtful. That of the proportional lengths of the nasal bones, for example, is justly disputed by Wagner.[1] Satisfactory evidence of the form of the pupil is hard to obtain, and does not appear to have any definite correlation with diurnal or nocturnal habits. The presence or absence of a caudal gland has been investigated in only a few species; and as it occurs in Wolves, Dogs, Jackals,[2] and Foxes, it is not likely to be of much importance. The proportions of the sectorial to the following teeth may be similar in Canidæ which are certainly not closely allied, and different in those which are. And the system of measurement hitherto usually adopted gives the absolute sizes of the teeth and their dimensions relatively to one another, but affords no clue to their proportions in relation to the size of the skull, or to the increase or diminution of individual teeth. The increase of the number of the teeth of *Otocyon* appears generally to be regarded merely as an anomaly.

[1] Schreber's Säugethiere, Suppl. Bd. ii. pp. 365, 384, notes.

[2] I have found a small caudal gland in a female *C. mesomelas*, which recently died in the Gardens.

There can be no doubt that the skulls and the teeth of the Canidæ vary from species to species more than any other part of their organization. One has only to put side by side with one another the skeleton of an *Otocyon* and that of a Wolf or that of a Fox, to see that the cranial and dental differences are very much greater than any which are observable elsewhere; and a glance at the skull and teeth of any other canine animal is sufficient to show that its characters give it a place somewhere between the former and the two latter. The problem therefore is how to give definite expression to the differences between *Otocyon*, Fox, and Wolf, and to determine by something better than vague eye-judgments the relation of the other forms to these.

2. When occupied with anthropological questions, a good many years ago,[1] I was confronted by the same kind of difficulty in endeavouring to arrive at an exact conception of the morphological relations of the skulls of the different races of mankind; and I was led to adopt a method of estimating cranial characters which still commends itself to me as that which is best calculated to meet the end in view.

Every constituent of the skull, like all other parts of the body, varies from individual to individual, and from youth to age. But the central region of the base of the skull, formed by the basioccipital, basisphenoid, and præsphenoid bones, represents the foundation around and upon which the other parts are built, and reaches its adult condition early. Moreover it answers to one of the most important parts of the central nervous system, the base of the brain. It is therefore eminently fitted to furnish a relatively fixed unit of measurement and standard of position, to which the dimensions and the position of the other parts of the head and face, with the teeth, can be referred.

In order to obtain such a standard, a median line is drawn in the bisected skull, from the hinder edge of the basioccipital bone to the junction between the præsphenoid and the ethmoid in the base of the skull. I call this line the ***basicranial axis***; and its value is taken as 100. The measurements of the other parts of the skull can then be expressed in terms of 100, and their development, irrespectively of the absolute size of the animal, becomes apparent. Sectional diagrams of different skulls, in which the basicranial axis has the same absolute length, show not only the different proportions of corresponding parts, but bring to light the relative depth, length, and inclination of the palate.

[1] "On two widely contrasted Forms of the Human Cranium," Journal of Anatomy, 1867.

This method of procedure is a little troublesome at first; but practice makes it easy, and the results are very satisfactory.

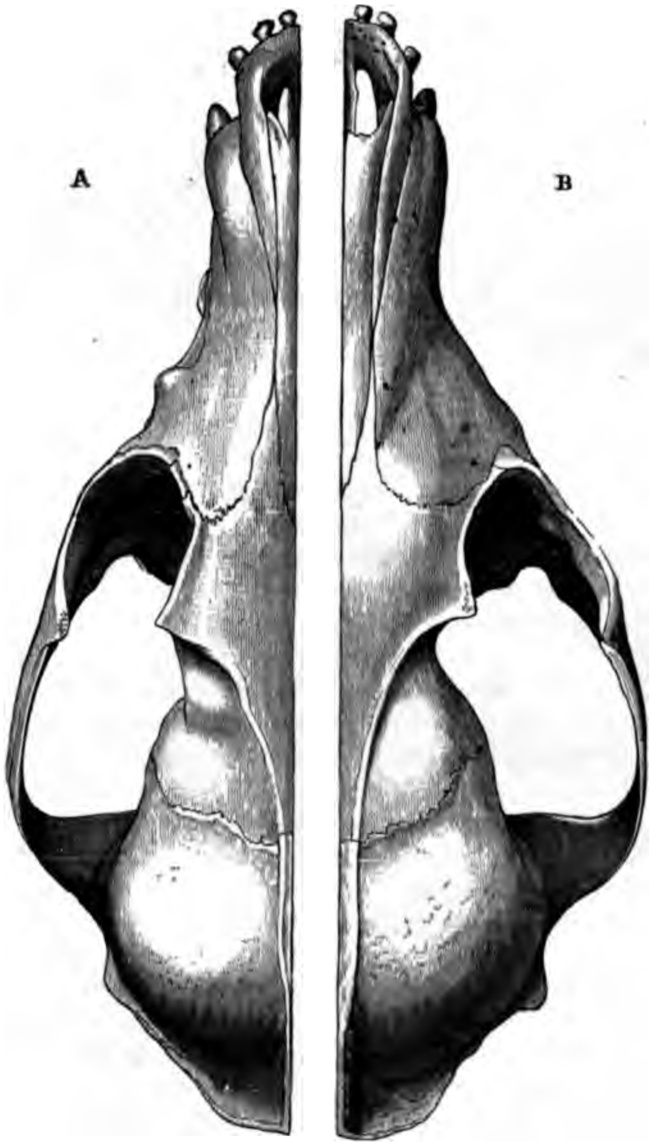


FIG. 1.—Dorsal view of the left half of the skull of *Canis azaræ* (A) and of the right half of the skull of *C. vulpes* (B), placed side by side. Natural size.

When, as often happens, the skull under examination cannot be bisected, a sufficiently close approximation to the true length of the basicranial axis may be obtained by taking the distance along the

median line of the base of the skull from the posterior edge of the basioccipital bone to a point opposite the middle of the distance between the optic and the ethmoidal foramina. This point always lies a little behind the posterior extremity of the vomer.

3. I will illustrate the method which I have described by comparing the skull of a common Fox with the skull of an animal which

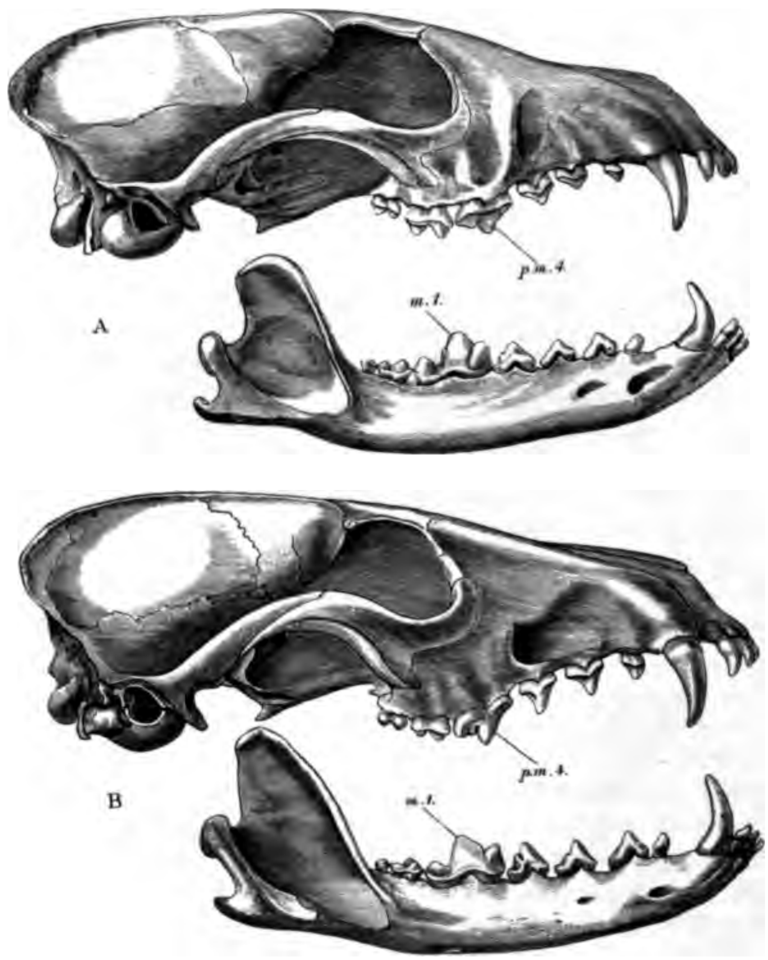


Fig. 2.—Lateral views of the skulls of *C. azaræ* (A) and *C. vulpes* (B). Reduced to two-thirds of the natural size.

died in the Zoological Society's Gardens, and came to me labelled "*Canis azaræ*, South America." It corresponds very closely with the skulls also assigned to *Canis azaræ* by De Blainville ("Ostéographie," *Canis*, pl. iv.) and by Burmeister ("Erläuterungen zur Fauna Brasiliens").

In their actual dimensions and in their general form these two skulls are very similar, except that the zygomatic arch of the European is stronger and more sharply arched than that of the South-American animal, and that the longitudinal contour of the face is straighter in the Fox, in consequence of a slight convexity of the interorbital and posterior nasal regions in *C. azaræ*. The ramus of the mandible of *C. azaræ* is somewhat deeper at the level of the last molar tooth, and its coronoid process is less high and less inclined backwards, while the ventral contour is more sinuous. Other minor differences will be obvious on comparison of the figures.

TABLE I.—*Measurements of the Skulls of* C. vulpes *and* C. azaræ.

	C. vulpes.	*C. azaræ.*
Total length	143	142
Zygomatic width	74	72
Length of bony palate	73	72
Width „ „	41	41
Length of basicranial axis	46	48
Length of the ramus of the mandible in a straight line from symphysis to condyle	109	105

[In this and the following tables of measurements "total length" means the distance from the front edge of the præmaxillary bones to the extremity of the occipital spine. The "zygomatic width" is the greatest transverse distance between the outer faces of the zygomatic arches. The "length of the bony palate" is measured from the front edge of the symphysis of the præmaxillary bones to the hinder edge of the middle of the bony palate, not taking into account the inconstant median spine which is frequently developed. The "width of the bony palate" is the distance between the points at which the outer faces of $\underline{pm. 4}$ and $\underline{m. 1}$ meet. The "length of the basicranial axis" has already been defined. The measurements are given in millimetres.]

The differences in the dentition between *C. vulpes* and *C. azaræ* are very slight. In the upper jaw of the Fox the series of the molar teeth of opposite sides slightly incline towards the middle line behind, while in *C. azaræ* they are almost parallel. Hence the angulation of the line of the cheek-teeth between the last præmolar and the first molar (fig. 3, A, B), is rather more marked in *C. vulpes*.

The præmolar teeth are smaller in *C. azaræ*; but as they are more worn it is difficult to make an exact comparison. The upper sectorial is not quite so long as that of the Fox. The transverse diameter is the same in front, but is less behind, in *C. azaræ*; and its inner cusp is less forward in position and less prominent. The lower sectorial is narrower and the anterior internal cusp somewhat larger in *C. azaræ*. In both, a line drawn from the anterior-external to the anterior-internal cusp (*a b*, fig. 3, p. 410) makes an acute angle with a transverse line, on account of the not very backward position of the latter.

In the Fox there is a very small secondary cusp between the inner anterior and the inner posterior cusps, which is absent in *C. azaræ*.

The second lower incisor lies completely behind the first in *C. azaræ*; but this is probably only an individual exaggeration of a

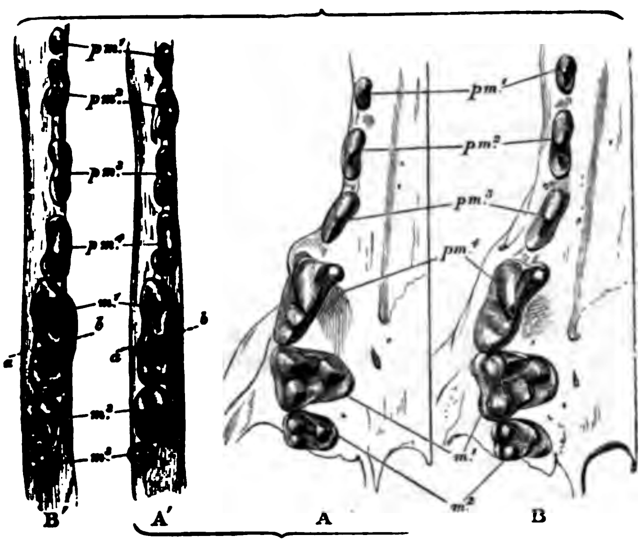


FIG. 3.—The crowns of the cheek-teeth of *C. azaræ* (A) and *C. vulpes* (B). Natural size. A, A', right upper and lower teeth of *C. azaræ*; B, B', the same of *C. vulpes*; *a, b* "cusp-line" traversing the apices of the inner and outer anterior cusps of $\overline{m.\ 1}$

tendency to the displacement of the second incisor backwards, which is often observable in the Canidæ.

TABLE II.—*Measurements of the Cheek-teeth of* C. vulpes *and* C. azaræ.

	C. vulpes.	*C. azaræ.*
Length of the whole upper præmolar and molar series	54	50
Length of the whole lower præmolar and molar series	60	57
Length of $\underline{pm.\ 4}$	13	12·5
" $\underline{m.\ 1}$	9·3	9
Breadth of $\underline{m.\ 1}$	11	11
Length of $\underline{m.\ 2}$	5	5
Breadth of $\underline{m.\ 2}$	7·3	7
Length of $\overline{m.\ 1}$	15	14·3
" $\overline{m.\ 2}$	7·3	7·5
" $\overline{m.\ 3}$	3	3·5

In both *C. vulpes* and *C. azaræ* the hinder ends of the nasal bones just reach the level of the hindermost part of the fronto-maxillary suture. In the Fox the ascending processes of the præ-

maxillary bones reach the anterior processes of the frontal bones while in *C. azaræ* there is a wide interval between the two.

In both, the temporal ridges unite into a crest for a short distance behind; but for the rest of their extent they are separate, inclosing a very narrow *sagittal area* (fig. 1, p. 407). At the anterior extremity of this the ridges diverge and pass outwards to the angles of the supraorbital process; and it is at this point that the principal external difference between the two skulls becomes apparent.

In the Fox (fig. 1, B, p. 407), the well-defined ridge runs nearly parallel with its fellow for some distance in front of the coronal suture, and then sweeps outwards, in a sharp curve, to the recurved supraorbital process, behind which a deep constriction marks the boundary between the interorbital and the temporal regions of the skull. In *Canis azaræ* the temporal ridge is not so well marked; and, beginning to diverge from its fellow a little in front of the coronal suture, it passes with a very slight curve to the angle of the supraorbital process, while the postorbital constriction is small (fig. 1, A). Moreover there is hardly any depression on the upper surface of the supraorbital process, the whole glabellar region being evenly arched from side to side. In the Fox, there is a well-marked depression on the outer part of the upper surface of the supraorbital process, and the glabella is flatter. These external differences answer to small but very definite distinctions which are seen in the longitudinal sections.

The superimposed sections of the two skulls correspond almost exactly.

In *C. vulpes*, as in all the Canidæ, the cribriform plate of the ethmoid bone is funnel-shaped, the concavity being turned towards the cranial cavity, while the convex surface looks outwards and upwards above, outwards and downwards below, into the nasal chamber. From its outer surface the delicate rolled laminæ of bone which answer to the superior and middle turbinals of human anatomy take their origin. The lower plates project backwards as far as the ethmo-præsphenoidal suture; while the upper ones reach as far back as the junction of the ethmoid with the frontal bones, and are covered over by the orbital and nasal prolongations of those bones. In *C. vulpes*, however, there are no frontal sinuses; that is to say, behind the point of union with the ethmoid the median parts of the thin frontal bones are solid throughout. Moreover, if, as in man, we distinguish that part of the frontal bone which covers the anterior surface of the cerebral hemispheres, from that part which lies further back, as the forehead, then the forehead of the Fox is very short, while the vertical height of the ethmoid is

proportionally great. In *Canis azaræ* there is a marked difference in all these respects (fig. 4, A, *f*). A large frontal sinus is developed in each frontal bone, above and behind the fronto-ethmoidal

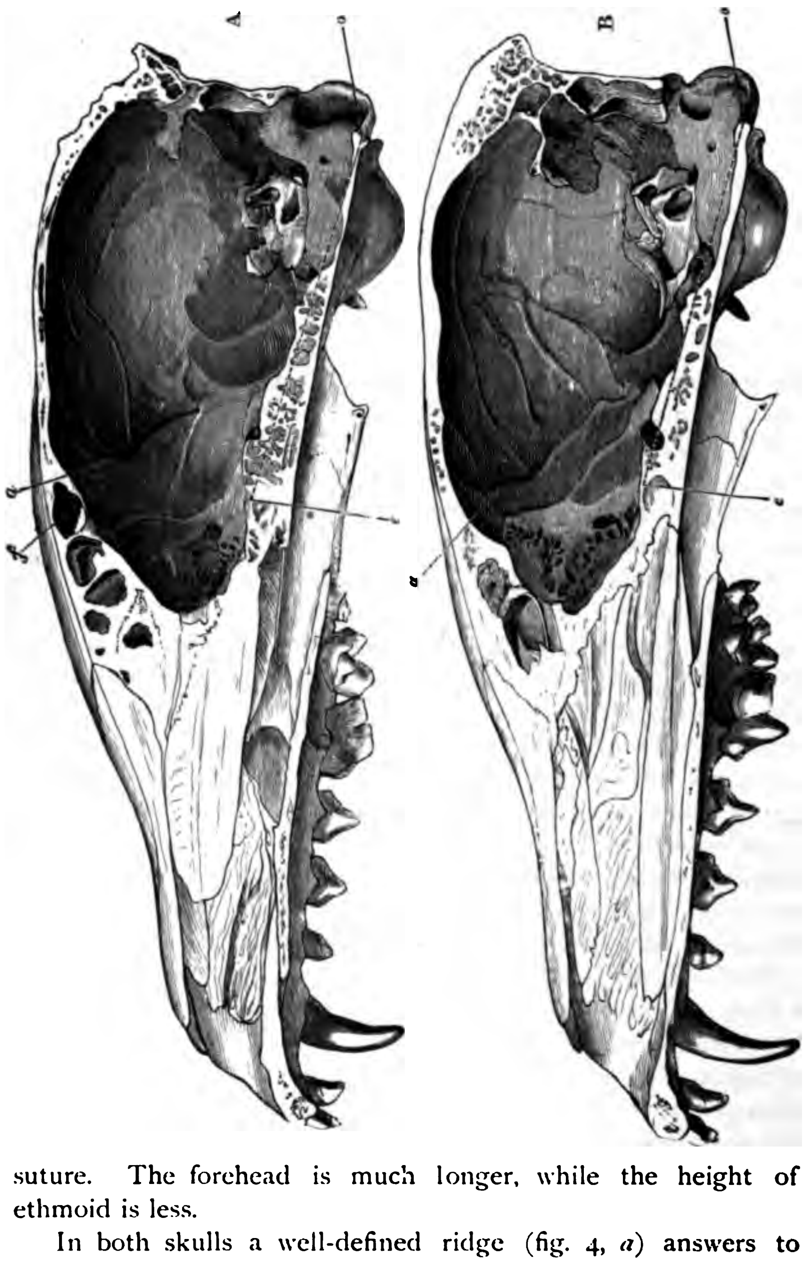


FIG. 4.—Longitudinal sections of the skulls of *C. azaræ* (A) and *C. vulpes* (B). *o c*, basicranial axis; *f*, frontal sinus; *a*, orbito-frontal ridge.

suture. The forehead is much longer, while the height of the ethmoid is less.

In both skulls a well-defined ridge (fig. 4, *a*) answers to the supraorbital sulcus, and marks off the region occupied by the curved

lateral gyri from that of the orbital and frontal gyri of the brain. But in the Fox this ridge (fig. 4, B, *a*) is directed upwards and forwards, and its dorsal end is separated by but a small distance from the dorsal margin of the cribriform plate of the ethmoid; while in *Canis azaræ* the dorsal half of the ridge (fig. 4, A, *a*) is inclined slightly backwards, and its end is far more remote from the edge of the cribriform plate. Moreover the inner wall of the skull is much more sharply bent inwards along the dorsal half of the orbito-frontal ridge than it is in the Fox.

These differences have their counterparts in the form of the brain, and become very manifest when casts of the interior of the skull are compared (fig. 5). In the Fox the contour of the brain, viewed from above, is that of a pear with the narrow end forwards. Laterally the contour-line is undulated, presenting one slight incurvation in the region of the sylvian sulcus and another in that of the supraorbital sulcus (fig. 5, *a*), while a little angulation (fig. 5, *b*, b_1) marks the junction of the olfactory lobes with the cerebral hemispheres. In *Canis azaræ* the cerebral hemispheres immediately behind the supraorbital fissure widen out abruptly (fig. 5, *a*), and the lateral contour, instead of being slightly incurved at this point, presents a sharp rectangular inflection. The frontal lobe anterior to the supraorbital sulcus is much longer in *C. azaræ* (*a–b′*) than in *C. vulpes* (*a–b*); and the brain is considerably wider behind in the latter.

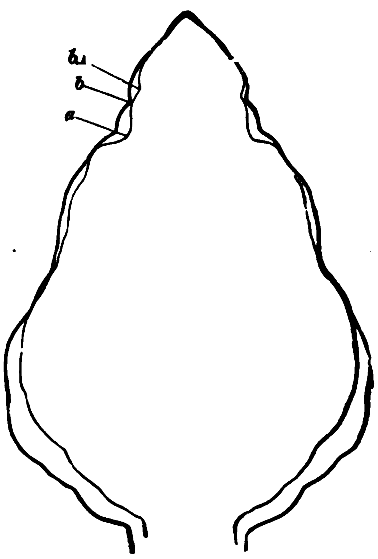


FIG. 5.—Superimposed outlines of the casts of the cranial cavities of *C. azaræ* and *C. vulpes*, viewed from above. The thin line belongs to the former, the thick line to the latter.

a, the supraorbital sulcus; *b*, the junction of the olfactory lobe with the cerebral hemisphere in *C. vulpes*; *b′*, in *C. azaræ*.

Thus, notwithstanding the extremely close resemblance of these two skulls, there is a very readily discernible difference between them in the presence of frontal sinuses and the peculiar character of the anterior part of the cranial cavity in *C. azaræ*, while both these features are absent in *C. vulpes*. These differences have nothing to do with size or age, inasmuch as the two skulls are almost identical in size and are both fully adult. Nevertheless I

do not know that I should have been disposed to attach any great importance to such characters, if I had not found, on examining a large number of canine animals, that they may be disposed in two groups, in one of which the peculiarities of *Canis vulpes*, while in the other those of *C. azaræ* are always to be met with.

Similar to *C. vulpes* are *C. fulvus*, *C. argentatus*, *C. cinereo-argentatus*, *C. littoralis*, *C. niloticus*, *C. caama*, *C. zerda*, *C. lagopus;* and, on the other hand, *C. lupus*, all varieties of *C. domesticus*,[1] *C. aureus*, *C. anthus*, *C. latrans*, *C. antarcticus*, *C. magellanicus*, and *C. cancrivorus* have the characters of *C. azaræ*.

We are thus enabled to distinguish two series of Canidæ, the one of which may be termed *Alopecoid* and the other *Thooid*.

The figures of the late Prof. Gervais, "Mémoire sur les formes cérébrales propres aux animaux carnivores" (Nouvelles Archives du Muséum, tome vi.), prove that the Thooid character of the brain obtains in *C. aureus*, *C. simensis*, *C. lupus*, *C. dingo*, *C. sumatrensis*, *C. primævus*, *C. jubatus*, and *Lycaon pictus*; while the Alopecoid features are very obvious in the Fennec.

4. But within each of these series there are considerable modifications, which give rise to corresponding terms in the two series.

The first of these modifications appears in the proportion of the sectorial and next following teeth relatively to the basicranial axis (= 100), shown by the following table in six examples of the Alopecoid series:—

TABLE III.—*Proportional Measurements of the Teeth in Alopecoids.*

	A.			B.			
	1.	2.	3.	4.	5.	6.	
Length of	*C. zerda.*	*C. littoratis.*	*C. famelicus.*	*C. vulpes.*	*C. niloticus.*	*C. argentatus.*	1 : 6
$\underline{pm.\ 4}$ . .	20·6	22·4	23·5	27·3	28·3	28·5	1 : 1·38
$\underline{m.\ 1}$ . .	17·3	18·1	18·	19·4	19·4	20·5	1 : 1·18
$\overline{m.\ 1}$ . .	24·	27·2	28·	30·5	31·1	34·4	1 : 1·43
$\overline{m.\ 2}$ . .	14·	15·7	13·5	14·7	14·4	15·0	1 : 1·07

These measurements represent individual specimens; and it must be recollected that others might vary considerably on either side of the proportions here given. But they suffice to prove, firstly, that in the group A the sectorial teeth are relatively smaller than in the group B, so that it may be convenient to speak of the one as *microdont*, and the other as *macrodont* Alopecoids; secondly, while $\underline{pm.\ 4}$, $\underline{m.\ 1}$,

[1] In a skull of a Blenheim Spaniel the frontal sinuses are totally absent, but the disposition of the orbito-frontal ridge is exactly as in other domestic Dogs. I do not know whether this peculiarity is general in the Blenheim breed or not.

$\overline{m.1}$, and $\overline{m.2}$ all become larger between *C. zerda* and *C. argentatus*, the increase is far greater on the part of $\underline{pm.4}$ than on that of $\underline{m.1}$ and of $\underline{m.1}$ than on that of $\underline{m.2}$. Thirdly, while in *C. zerda* $\underline{m.1}$ is to $\underline{pm.4}$ as 1 : 1·19 and $\overline{m.2}$ to $\overline{m.1}$ as 1 : 1·71, in *C. argentatus* the former proportion is 1 : 1·39 and the latter as 1 : 2·26. In other words, in the macrodont Alopecoids these teeth are not merely larger but they are

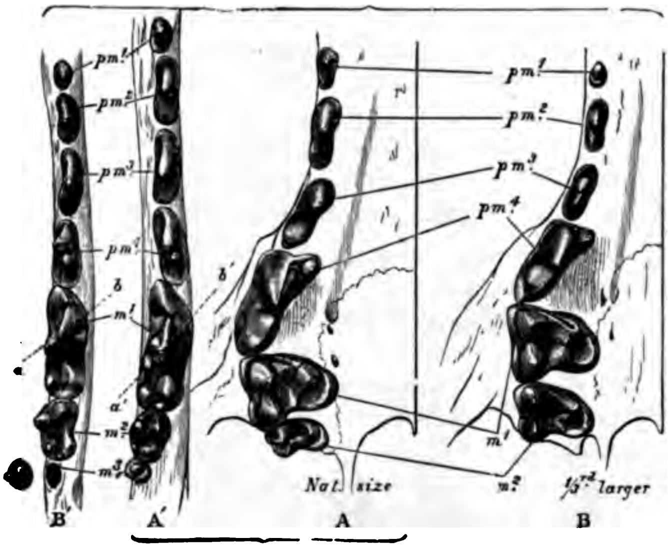


FIG. 6.—The crowns of the cheek-teeth of *C. argentatus* (A, A′) and *C. littoralis* (B, B′). Those of *C. argentatus* are of the size of nature; those of *C. littoralis* are enlarged in the proportion of 4 : 3, and consequently are larger by one-third than the natural size. This enlargement has the advantage of giving the same length to $\underline{m.1}$ in both, and thus enabling the relative dimensions of the teeth to be seen. At the same time, inasmuch as the length of the basicranial axis in the skull of *C. argentatus* is to that in *C. littoralis* as about 4 : 3, the figures fairly represent the actual morphological relations of the teeth.

a b, *a′ b′*, cusp-lines of the lower sectorial teeth. The third lower molar in B′ was absent, and is figured from another specimen; its crown is seen somewhat obliquely.

more differentiated, the sectorial teeth becoming increased out of proportion to the rest.

Similar relations are observable in the Thooid series, as the following table of proportional measurements clearly shows:—

TABLE IV.—*Proportional Measurements of the Teeth in Thooids.*

	A		B			
Length of	1. *C. azaræ* (a).	2. *C. magellanicus.*	3. *C. azaræ.*	4. *C. dingo.*	5. *C. lupus.*	1 : 5
$\underline{pm.4}$	22·4	24·4	26·3	30·	32·5	1 : 1·45
$\underline{m.1}$	17·7	15·9	19·4	20·	23·2	1 : 1·31
$\overline{m.1}$	27·7	26·5	30·0	33·2	36·9	1 : 1·33
$\overline{m.2}$	14·4	12·2	15·7	14·4	17·1	1 : 1·18

In this series $\frac{pm.4}{}$ and $\frac{}{m.1}$, as before, increase out of proportion to the rest, and $\frac{}{m.2}$ undergoes the least alteration ; but the upper sectorial increases rather more than the lower, which is the reverse of the relation which obtains in the Alopecoid series.

5. In all young canine animals, the upper edges of the attachments of the temporal muscles are separated by a wide interspace of a lyrate form, with its apex directed posteriorly, which may be called the *sagittal area.* The boundaries of this area are but little raised ; and, as age advances, it becomes gradually diminished by the approximation of the temporal muscles. This approximation takes place more rapidly behind than in front, and results in the narrowing, and in most cases coalescence, of the temporal ridges throughout the greater part of the length of the sagittal suture, while in front

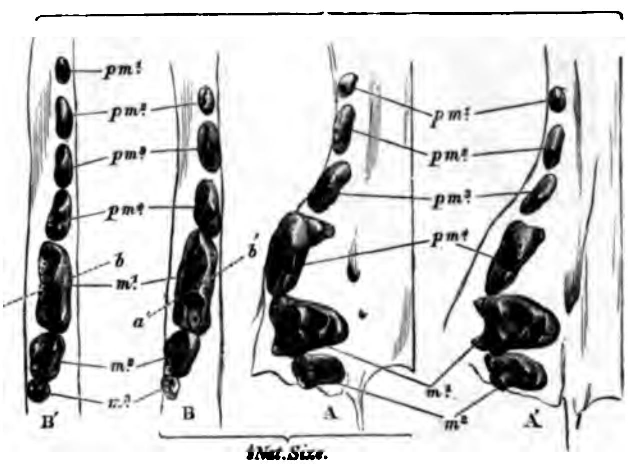


FIG. 7.—Upper (A) and lower (B) cheek-teeth of *C. lupus*, half the natural size; upper (A′) and lower (B′) teeth of *C. azaræ* (a), of the natural size. The first upper molars are thus brought to the same length, and the proportional increase of size of the sectorial teeth of the Wolf is apparent.

they diverge to the supraorbital processes and inclose the glabellar area.

In the smaller Alopecoids, such as *C. zerda*, the temporal ridges remain permanently separate, and inclose a wide lyrate sagittal area, the ridges themselves not being very strongly marked; but in *C. littoralis* and *C. cinereo-argentatus* (= *C. virginianus*) the ridges take the form of strongly-raised cord-like elevations, which impart a very characteristic aspect to the skull (fig. 8, p. 417). In this case there is no sagittal crest. But sometimes there is a well-defined though comparatively narrow sagittal area, from the centre of which

a low sagittal crest rises. This is well seen in some Jackals, and especially in *C. antarcticus.*

6. In most of the Alopecoids, the contour of the inferior margin of the angular process continues the direction of that of the inferior

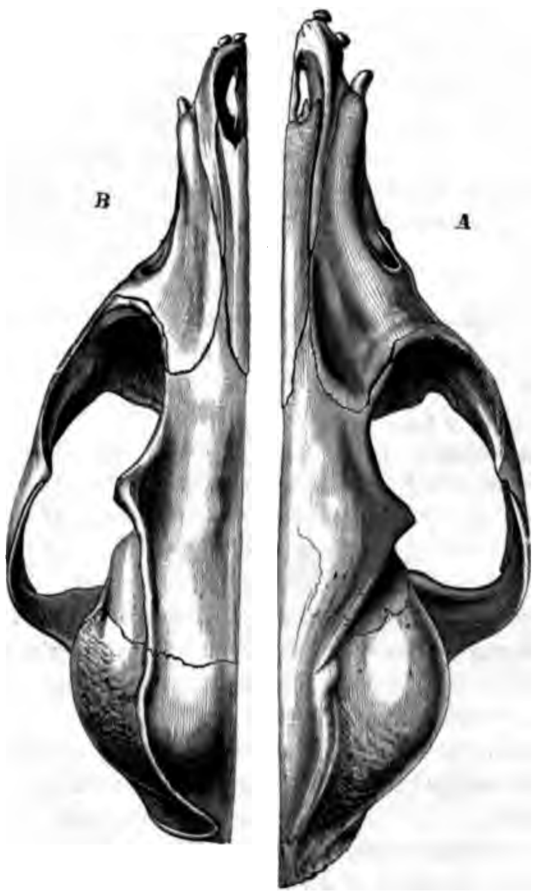


FIG. 8.—A, Dorsal aspect of the right half of the skull of *C. azaræ* (a); B, the same of the left half of *C. littoralis*: of the natural size.

margin of the ramus in front of it; and this slopes gradually upwards and backwards. In *C. littoralis* and *C. cinereo-argentatus*, however, the inferior contour of the ramus in the region of the attachment of the digastric muscle, in front of the angular process, is inclined almost at right angles to the latter, and forms a sort of rounded "subangular lobe" beneath the angular process. De Blainville long since figured and called attention to this feature of the mandible in *C. cinereo-argentatus.*

These peculiarities are closely reproduced in the Thooid series, by the skull of a South-American animal referred to *Canis azaræ*,[1] which died in the Gardens of the Society, and to which I have alluded above as *C. azaræ* (a) (fig. 8 A, p. 417). The sagittal area is wide and lyrate ; but the temporal ridges are not so strongly marked as in *C. littoralis*. There are no strong depressions on the supraorbital processes ; and the glabella is evenly arched, in correspondence with the small but distinct frontal sinuses. The angular process of the mandible is extremely strong, and its margin is thick and tumid. Beneath it there is a well-developed subangular lobe (fig. 9 A, L).

The following table of proportional measurements (basicranial axis = 100) shows how closely *C. azaræ* (a) and *C. littoralis* represent one another.

TABLE V.—*Proportional Measurements of the Skull and Teeth of* C. azaræ (*a*) *and* C. velox.

	C. azaræ (a).	*C. velox*.
Total length of bony palate	125	122
" breadth of "	78·9	71
" length of $\underline{\text{pm. 4}}$	22·4	22·4
" " $\underline{\text{m. 1}}$	17·7	18·1
" " $\underline{\text{m. 2}}$	11·1	13·3
" " $\overline{\text{m}}$	27·7	27·2
" " $\overline{\text{m. 2}}$	14·4	15·7

In both, a small accessory cusp is developed on the posterior part of the outer face of the external anterior or principal cusp of the lower sectorial tooth (fig. 9 A and B).

Nevertheless the frontal sinuses and the form of the anterior part of the cerebral cavity at once distinguish *C. azaræ* (a), as a Thooid, from *C. littoralis*.

7. The transition between *C. azaræ* (a) and the macrodont Thooids is furnished by the skull of an animal from Pernambuco, which died in the Gardens, and came to me labelled *C. fulvipes* (fig. 10, p. 420). The sagittal area is much narrower than in *C. azaræ* (a) ; and the temporal ridges unite into a short median crest behind. The glabella is convex, and the postorbital constriction small, in correspondence with the considerable development of the frontal

[1] Mr. Forbes informs me that this animal possessed a short straight cæcum. *C. cancrivorus* has a similar cæcum. In *C. procyonoides*, *C. jubatus*, and *Icticyon venaticus* the cæcum is longer and larger, but almost straight. In all the other Canidæ (certainly in *C. lupus*, *C. laniger*, *C. domesticus*, *C. aureus*, *C. anthus*, *C. antarcticus*, *C. azaræ*, in *Cyon*, *Lycaon*, *Vulpes*, and *Otocyon*) it would appear that the cæcum is large and coiled. (See Garrod, P.Z.S. 1873 and 1878 ; Murie, P.Z.S. 1873 ; Flower, P.Z.S. 1880.)

sinuses. The angular process of the mandible (fig. 9, C, A) is deep, strong, and thick, but not tumid as in the foregoing species.

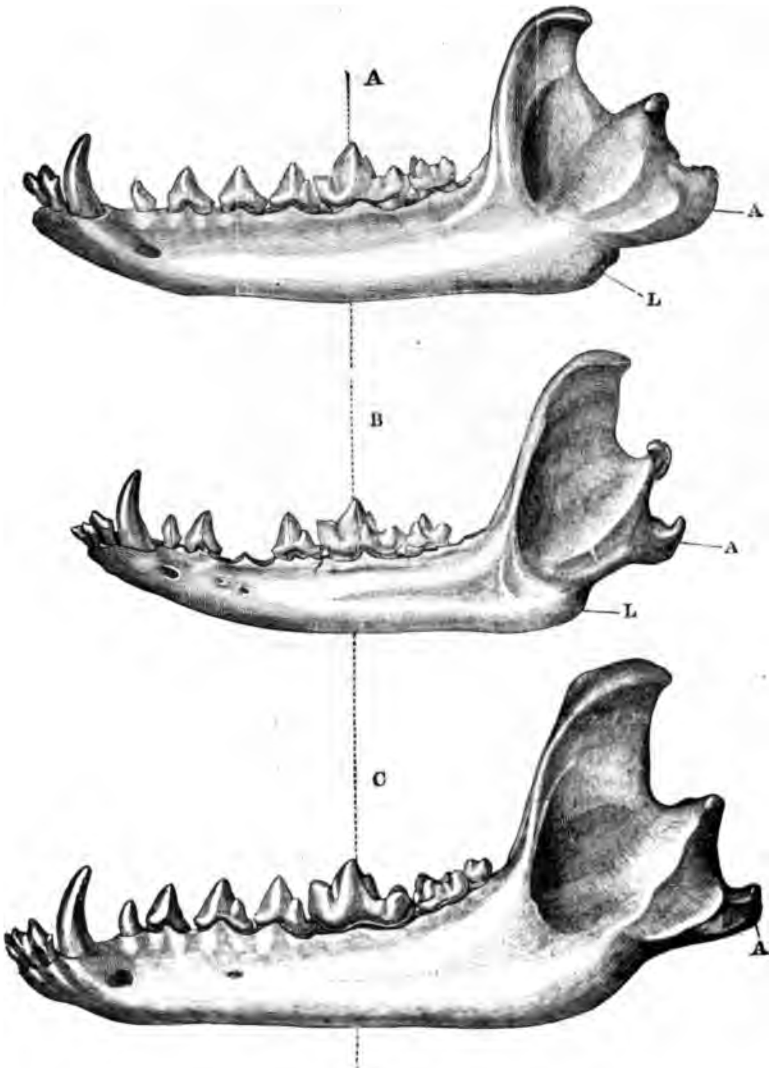


FIG. 9.—The left ramus of the mandible.
A. *C. azaræ* (a); B. *C. littoralis*; C. *C. fulvipes*: of the natural size.
A, angular process; L, subangular lobe.

The subangular lobe is far less developed; hence the inferior contour of this part of the jaw is not very much more prominent than it is in some of the Jackals.

I cannot distinguish the skull of this "*C. fulvipes*" from that figured by De Blainville ("Ostéographie," *Canis*, pl. viii.) under the name of *Canis cancrivorus*, from Cayenne—nor from the *C. cancrivorus* of Burmeister, which appears to be identical with the *C. bra-*

FIG. 10.—Dorsal view of the skull of *C. fulvipes*.

siliensis of Lund. Under these circumstances I presume that it should be named *C. cancrivorus*.

Another skull of a male animal which died in the Gardens has unfortunately lost its mandible. It is labelled "*C. cancrivorus*," and differs from the foregoing only in having a much broader sagittal area, with slightly larger teeth and broader and longer

palate in proportion to the basicranial axis (though not absolutely), than the foregoing.

A third skull, also labelled "*C. cancrivorus*," ♀, is young, with the milk-teeth not yet shed. The permanent first molars above and below are just coming into place; and their actual dimensions are so nearly identical with those of the preceding skulls, that, though the mandible has not quite the characteristic degree of lobation, I am disposed to think that the differences which exist depend merely on age.

8. If the measurements of the skulls of *C. azaræ* (a), *C. cancrivorus*, and *C. azaræ* be now compared with one another and with those of *C. aureus*, *C. anthus*, and *C. lupus*, they will be found to form a gradual series of modifications.

TABLE VI.—*Proportional Measurements of the Skulls and Teeth of* Thooids.

	C. azaræ. (a).	*C. cancrivorus.*	*C. azaræ.*	*C. aureus.*	*C. anthus.*	*C. lupus.*
Length of basicranial axis	100	100	100	100	100	100
Length of $\underline{pm.\,4}$	22·4	25·5	26·3	27	30	32·5
" " $\underline{m.\,1}$	17·7	20·8	19·4	21·4	20·4	23·2
" " $\underline{m.\,2}$	11·1	12·5	12·1	12	13·6	12·5
" " $\overline{m.\,1}$	27·7	29·1	30	30·9	34	36·9
" " $\overline{m.\,2}$	14·4	15·6	15·7	17·1	16·3	17·1
" " palate	125	125	150	124	137	146
Breadth of palate	78·9	79	85	94	95	99

The only considerable break in the regularity of the progression here arises from the large size of $\underline{m.\,1}$ in *C. cancrivorus* and the unusual length of the palate in *C. azaræ*. This regularity, however, is fortuitous. The measurements here given are those of individual skulls; and if several individuals of any given species are measured in the same way, the range of variation in some cases is remarkable. Thus, three specimens of the Indian Jackal yield the following results (basicranial axis = 100):—

TABLE VII.—*Proportional Measurements of Teeth and Palate of* Canis aureus.

	I.	II.	III.
Length of $\underline{pm.\,4}$	27	31	33·8
" " $\underline{m.\,1}$	22	24	21·6
" " $\underline{m.\,2}$	12	12·2	13·2
" " $\overline{m.\,1}$	30·5	34	35·8
" " $\overline{m.\,2}$	17	16·9	16·6
" " $\overline{m.\,3}$	—	7·5	7·5
Length of palate	125	141	143
Breadth of palate	94	90	90

The actual dimensions in millimetres are as follows :—

TABLE VIII.—*Cranial and Dental Measurements of* Canis aureus.

	I.	II.	III.
Length of basicranial axis . . .	59	53	53
" $\underline{pm.\ 4}$	16	16·5	18
" $\underline{m.\ 1}$	13	13	11·5
" $\underline{m.\ 2}$	7	6·5	7·1
" $\overline{m.\ 1}$	18	18	19
" $\overline{m.\ 2}$	10	9	9
" $\overline{m.\ 3}$	—	4	4
" palate	74	75	76
Breadth of "	56	48	48

The comparison of these two tables is interesting ; for, according to the first, the variations of the dimensions of the teeth in proportion to those of the basicranial axis cover the whole range between *Canis azaræ* and the Wolves ; on the other hand, the second shows that, while the basicranial axis, doubtless following the actual size of the animal, varies considerably, and while the teeth also vary, the two sets of variations do not correspond : hence, in the proportional table, the differences in the sizes of the teeth appear to be greater than they really are.

Similar results are attained when the measurements of any considerable number of specimens of other canine skulls are compared. In fact, while in both the Thooid and the Alopecoid series the species may be arranged in a scale characterized by the gradually increasing relative and actual dimensions of the sectorial teeth, each species occupies not a line but a broad zone upon that scale, which zone is overlapped by that of the species below and by that of the species above.

9. The lowest Alopecoids and the lowest Thooids agree in the relatively small size of their sectorial teeth ; and many possess a large lyrate sagittal area and a strongly lobate mandible. The genus *Otocyon* shares the last two peculiarities, and exhibits the first in a more marked degree than any other known canine animal, recent or extinct.

There are three skulls of this interesting form in the Museum of the Royal College of Surgeons, and three in the British Museum ; and they all agree very closely with the figures and description given by De Blainville.

In all, the posterior ends of the nasal bones extend beyond the fronto-maxillary suture ; but they vary considerably in width. The frontal processes are well separated from the ascending processes of

the præmaxillaries. The temporal ridges are much stronger and the sagittal area narrower in one skull, which appears to be the oldest. There are no frontal sinuses. In all, the subangular lobe of the mandible is very strong, thickened, and more or less incurved at its free margin. The angular process is strong, and projects inwardly

FIG. 11.—Dorsal view of the skull of *Otocyon lalandii*: nat. size.

as a horizontal shelf-like prominence, which is concave above, so that it somewhat resembles the bowl of a spoon (fig. 14, C, p. 430).

The posterior margin of the bony palate lies considerably behind the line of the hindermost molars. The line of the cheek-teeth is not angulated at the junction of the upper sectorial with the first molar, but nearly straight and almost parallel with that of the opposite side (fig. 13, B, p. 426). The incisive foramina are prolonged forwards

into deep grooves on the palatal surfaces of the præmaxillæ. The incisor teeth have different proportions from those of ordinary Canidæ, the outer being relatively smaller and less different from the rest. The outer upper incisor, on each side, is separated by an interval from the second.

The great difference between *Otocyon* and all the other Canidæ, however, lies not merely in the increased number of the molar teeth, but in the proportions of the teeth to the basicranial axis and to one

FIG. 12.—Lateral view of the skull of *Otocyon lalandii* : $\frac{3}{4}$ nat. size.

another, and in the low development of the jaws. The following table gives the average of three of the skulls :—

TABLE IX.—*Proportional Measurements of the Skull and Teeth in* Otocyon.

Basicranial axis	100 (average absolute length 42 mm.)
Length of $\underline{pm.\ 4}$	12·7
„ „ $\underline{m.\ 1}$	13·4
„ „ $\underline{m.\ 2}$	11·8
„ „ $\overline{m.\ 1}$	16·1
„ „ $\overline{m.\ 2}$	13·3
„ „ $\overline{m.\ 3}$	9·8
„ palate	138
Breadth of palate	66

Thus the upper jaw is both short and narrow ; and the slenderness of the rami of the mandible is not less remarkable, though in this respect *C. cancrivorus* and *C. procyonoides* approach *Otocyon.*

TABLE X.—*Cranial and Dental Measurements of* Otocyon lalandii.

	I.	II.	III.	IV.	V.	VI.
Total length	114	123	112	113	112	—
Length of palate	57	61	53	54	58	59
Breadth „	28	26	27	27	29	27
Length of basicranial axis . .	—	—	40	41	43	41
Length of $\underline{pm.\,4}$	5·7	6·5	5·5	5·3	5·5	5
Breadth „ in front . . .	5	5·5	5·8	4·7	5	4
Length of $\underline{m.\,1}$	5	5·5	5	5·5	6	5
Breadth „	6·2	8	7	6	7	6·5
Length of $\underline{m.\,2}$	5	5·5	5	5	5	4·5
Breadth „	6·5	8	7	6·5	6·5	6·5
Length of $\underline{m.\,3}$	4·5	5	4	3·5	4·5	4
Breadth „	6	6	6	5	5·5	5·5
Length of $\underline{m.\,4}$	—	—	—	—	—	4
Breadth „	—	—	—	—	—	4
Length of $\overline{m.\,1}$	6	7	6·5	6·5	7	6
„ $\overline{m.\,2}$	6	6	6	5·5	6	5
„ $\overline{m.\,3}$	5	6	5	4·3	4·5	4
„ $\overline{m.\,4}$	3·5	4	3	3	3·3	*

* Fallen out on both sides.

On inspection of the foregoing tables of the actual and the proportional measurements of the skulls and teeth, the wide differences between *Otocyon* and all the other Canidæ become apparent.

Confining our attention for the present to those teeth in *Otocyon* which answer to those met with in other Canidæ, it is obvious that the sectorial teeth are much smaller in proportion to the basicranial axis, that the difference between $\overline{m.\,1}$ and $\overline{m.\,2}$, $\overline{m.\,2}$ and $\overline{m.\,3}$, is much less, and that $\underline{pm.\,4}$ is never greatly longer and may be shorter than $\underline{m.\,1}$.

The patterns of the crowns of the upper cheek-teeth (fig. 13, B) are completely canine. The anterior inner cusp of the fourth upper præmolar is very thick and prominent, and gives the crown of the tooth the form of an almost equilateral triangle. There is a well-developed secondary cusp at the anterior end of the base of the principal cusp of this tooth, so that, viewed from the outside, it appears tricuspidate; and sometimes there is a minute cusp behind the principal inner cusp. In both points this tooth approaches the upper sectorial of *Nasua*. The crowns of the molars are broader than they are long; but the difference is less than in most Canidæ. Their four cusps, with the cingulum on the inner side, are very distinct; and the second upper molar is much larger in proportion to the first than in other Canidæ.

In the mandible, the third præmolar has a sharp cusp at the anterior end of its base; the first molar has the inner cusps higher than the outer ones; and the anterior paired cusps are set in a nearly transverse line, the inner hiding the outer when the tooth is viewed from within (fig. 13, C). In both these respects the crown of this tooth differs from that of other Canidæ and approaches the characters of the same tooth in the Viverridæ and, especially, in the Procyonidæ.

It is obvious that, in all these features, *Otocyon* represents a lower term in the series of the Alopecoids than *C. cinereo-argentatus* and

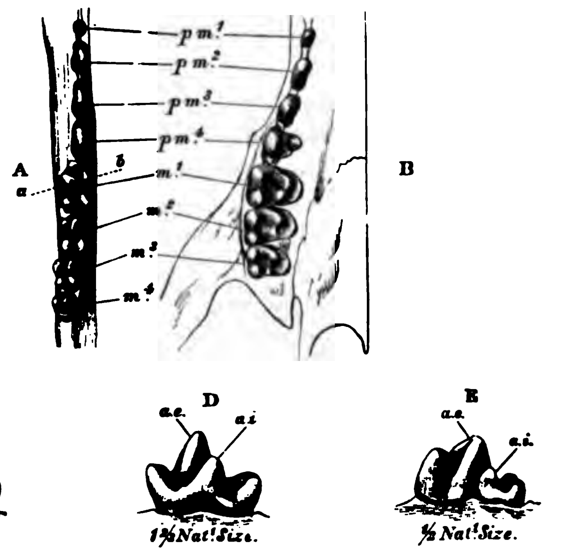


Fig. 13.—A, lower, and B, upper cheek-teeth of *Otocyon lalandii*; the last molar in the upper jaw is absent; C, the lower sectorial tooth of *Octocyon* from the inner side, of twice the natural size; D, the corresponding tooth of *C. zerda*, and E. of *C. lupus*, reduced to the same absolute length and also viewed from the inner side; *a.e.* anterior external cusp; *a i.* anterior internal cusp; *a.b.* cusp-line. The tooth of the Fennec is obviously intermediate in character between that of *Otocyon* and that of the Wolf. The comparison of these figures with figs. 6 and 7 will give a very good conception of the extent and the nature of the modifications of the cheek-teeth in the Canidæ.

C. velox; and although the interval between these and *Otocyon* is as wide as that between *C. velox* and *C. vulpes*, there would be no reason for separating *Otocyon* from the rest of the group were it not for the extraordinary excess in the number of molar teeth. Of these there are four on each side above in one specimen, three in the others, four on each side below in all. So far as any conclusion can be drawn from this limited number of examples, therefore, it would appear that the presence of the fourth upper molar is exceptional;

and that the dentition is tending towards a higher type by its suppression. The crowns of the hindermost upper molars, in the one specimen in which they are shown, are of a triangular shape, the base of the triangle corresponding with the two distinct external cusps. On the inner side only one cusp remains. The crown of the small fourth lower molar exhibits two well-developed cusps, of which the outer is rather the smaller. These apparently represent the anterior cusps of the other molars, as the posterior pair of cusps are proportionally smaller than the anterior pair in the third molar.

10. The facts now adduced appear to me to permit of the arrangement of the Canidæ hitherto considered in the following manner:—

CANIDÆ.

I. *Molars* $\frac{2\cdot2}{3\cdot3}$.

A. Alopecoids.	B. Thooids.
a. Macrodonts.	
Ex. *C. argentatus.*	Ex. *C. lupus.*
C. vulpes.	*C. aureus.*
b. Microdonts.	
α. Mandible nonlobate.	
Ex. *C. caama.*	Ex. *C. azaræ.*
C. zerda.	*C. vetulus.*
β. Mandible lobate.	
Ex. *C. littoralis.*	Ex. *C. cancrivorus.*

II. *Molars* $\frac{4\cdot4}{4\cdot4}$.

C. Otocyonoids.
Otocyon.

It will, however, be readily understood from what has already been said, that it is not intended to suggest the possibility of sharply separating the macrodont from the microdont forms, or those with lobed mandibles from those with mandibles of the ordinary character. On the contrary, they pass into one another; while the lower Thooids, with small frontal sinuses, are so slightly separated from the lower Alopecoids, that it is hard to say whether we have any right to look for a Thooid representative of *Otocyon* or not. It is quite as reasonable to suppose that *Otocyon* is the nearest living representative of the primitive type of the Canidæ, whence all the rest have been derived, in the first place, by the differentiation of the Thooid from the Alopecoid series, and, in the second, by the occurrence of corresponding series of modifications leading up to the Fox on the one hand and to the Wolf on the other.

11. If this view of the facts is correct, the key to the morphological relations of the whole of the Canidæ must lie in the determination of the affinities of *Otocyon*. The facts hitherto considered primarily appear to me to suggest looking in two directions—in the first place towards the Procyonidæ, and in the second towards the Didelphia.

In studying the Canidæ it is impossible not to be struck by the wonderful persistency of the fundamental patterns of the sectorial teeth and of those which follow them. This singular uniformity can hardly be accounted for by adaptation to similar modes of life; for the pattern is as distinctly marked in *C. jubatus* and *C. procyonoides*, which live largely upon fruits and roots and never attack large animals, as in any of the more purely carnivorous Canidæ. It must therefore be regarded as a morphological fact of fundamental importance, and the best guide to the immediate affinities of this group of animals.

Now, in *Bassaris* we have a procyonine form, the teeth of which are extraordinarily similar to those of *C. zerda*, if we suppose the little posterior lower molar of the Fennec suppressed. The posterior margin of the bony palate is on a level with the hindermost molar teeth, and therefore does not extend further back than in the ordinary Canidæ. There are no frontal sinuses; and the ethmoid is high. In *Ælurus*, again, the patterns of the teeth are essentially canine, though inclining in some respects towards the Bears: the frontal sinuses are large, the ethmoid low, and the cranial cavity has a completely Thooid contour. In this genus, as Prof. Flower has pointed out, an alisphenoid canal is present. The small flattened bulla, with its long meatus, is unlike that of the Dogs; on the other hand, the carotid canal is long, and its posterior aperture opens into a depression common to it and the foramen lacerum posterius. The bony palate extends considerably further back than in any existing canine animal.

In *Nasua* the fourth præmolar above is triangular; but a small second inner cusp is beginning to appear behind the large one. In *Procyon* this cusp has increased so much that the crown of the tooth is quadrangular. In this genus there is a small cingulum on the inner side of the first and second molars, which thus retain a resemblance to those of the Dog. In *Nasua*, however, it is no longer visible. In both these genera a line joining the inner and outer cusps of the lower sectorial teeth is almost transverse to the axis of the tooth, and the inner cusp is higher than the outer, as in *Otocyon*.

I find the proportional lengths of the teeth in *Nasua* and *Procyon* to be as follows:—

TABLE XI.—*Proportional Length of the Teeth in* Procyonidæ and Otocyon.

	Nasua.	*Procyon.*	*Otocyon.*
Length of $\underline{pm.\,4}$	16·6	16·6	12·7
" $\underline{m.\,1}$	17·7	17·7	13·4
" $\underline{m.\,2}$	16	12·7	11·8
" $\overline{m.\,1}$	18·8	20·5	16·1
" $\overline{m.\,2}$	20	19·4	13·3

The teeth of *Nasua* and *Procyon* are larger (and notably thicker) than those of *Otocyon*; moreover the hindermost molars, in their elongation and in other characters, tend towards the Ursine form. There is therefore no question of direct affinity between *Nasua* and *Procyon* and *Otocyon*; it is simply that, in dental characters, the lowest type of canine animal approaches the less-differentiated Procyonidæ.

In *Bassaris* and in *Procyon* the form of the ramus of the mandible is similar to that in the ordinary Canidæ; in *Nasua* it approaches that seen in *C. cancrivorus*; in *Ælurus* this peculiarity is still more exaggerated; and in *Cercoleptes* we have a mandible which resembles that of *Otocyon*, with a still more developed lobe. As to the base of the skull, it appears to me that, taking *Ælurus*, *Procyon*, and *Nasua* together, the arctoid characters are so modified, and the approximation to the canine type of skull becomes so close, that they almost present a transition from the one type of skull to the other.

I have elsewhere drawn attention to the fibrous epipubis of the Dogs as the homologue of the so-called "marsupial bone" of the Didelphia and Ornithodelphia,[1] and other indications of the approximation of the lower Carnivores to the *Didelphia* are not wanting.

If the mandibles of *Otocyon*, of *Procyon*, and of *Perameles* are viewed from behind (fig. 14, p. 430), it will be seen that the angular process is as distinctly inflected in the two former as in the latter, and

[1] Proceedings of the Royal Society, 1879. I have recently found the epipubis very well developed in a female Bengal Fox and in a female *C. mesomelas*. My friend Dr. Rolleston, F.R.S., has been good enough to compare *Thylacinus* with the domestic Dog; and he informs me that "the bone is disproportionately small in the marsupial in question; but it has precisely the same relation to the external oblique's bifid tendon, to the rectus and pyramidalis (which are only imperfectly differentiated from one another and from the inner or upper division of the tendon of the external oblique), and, finally, to the pectineus, which it has in the placental mammal."

that the difference in the angular process of *Thylacinus* is merely one of the degree of development of a homologous and similarly formed part.[1]

I look upon the four molars of *Otocyon* as another character of the same order; as a survival, in fact, of a condition of the dentition exhibited by the common ancestors of the existing Canidæ and the existing carnivorous marsupials.

12. The geographical distribution of the Canidæ presents many points of interest when it is considered in relation to the morphological characters of the forms at present restricted to certain areas of the earth's surface.

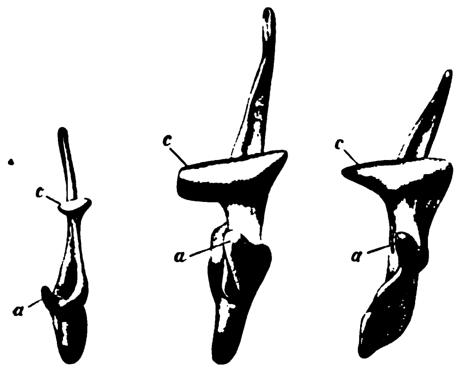


FIG. 14.—Right ramus of the mandible of *Perameles* (A), *Procyon* (B), and *Otocyon* (C), from behind: *a*, angular process; *c*, condyle.

Otocyon occurs only in South Africa, and apparently does not range beyond the southern extremity of that continent.

The microdont Alopecoids with lobate jaws (*C. cinereo-argentatus* and *C. littoralis*), which have been separated by Baird under the name of *Urocyon*, appear to me to be the nearest existing allies of *Otocyon*. But there is no representative of this group outside the North-American continent, *C. cinereo-argentatus* occupying the central States of North America, while *C. littoralis* occurs on the N.W. in California, and on the south as far as Honduras and Costa Rica. Baird suggests that *C. littoralis* is merely a local race of *C. cinereo-argentatus*; and the measurements in Table XII., which show that No. II. is as near to No. III. as to No. I., lend strong support to this view.

The small Foxes of the Old World, *C. zerda* and *C. caama*, differ from the foregoing in little more than the non-lobation of the mandible and the less prominent or cord-like character of the temporal ridges. In *C. bengalensis*, *C. corsac*, and *C. velox* the sagittal area narrows and the temporal ridges unite behind, while the sectorial teeth increase in proportional size, and thus gradually lead to the most specialized Foxes of the Old World.

[1] A comparison of the mandible of *Didelphys* with that of *Nasua* is even more instructive. In *Centetes* the angular process is slightly but characteristically inflected.

TABLE XII.—*Cranial and Dental Measurements of* Alopecoids.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.
Total length	97	104	—	84	108	—	112	112	126	—	136	143	146
Length of palate	45	51	57	42	50	53	60	60	64	63	67	73	74
Breadth „	27	29	34	25	33	30	32	34	40	38	40	41	44
Length of basicranial axis . .	36	38	45	36	42	39	38	—	44	—	49	46	50
„ $\underline{\text{pm. 4}}$	8·5	10	11	8	9	9·5	11	11	12·5	13	13	13	15
„ $\underline{\text{m. 1}}$	5·5	7·5	9	6	8	8	7	8	9	8·5	9	9·3	10·5
Breadth „	7·5	8·5	6	7 7	10	—	8	8·5	10·5	—	11	11	11·5
Length of $\underline{\text{m. 2}}$	4·5	5·5	6	4	5·5	5	4	4	5	4	5	5	5·5
Breadth „	5·5	6·5	—	6	8	—	6	7	7·5	—	7	7·3	7·5
Length of m. 1	9·5	11·5	12·5	8·5	11	10	11·5	13·5	14	14	15	15	17
„ $\overline{\text{m. 2}}$	5	6	7·5	5	6	6·5	5·5	6·5	6·5	6	7	7·3	7
„ $\overline{\text{m. 3}}$	2·6	—	—	2·5	—	3	2	2·6	3	—	3·5	3	3

[Nos. I. and II. *C. littoralis*; No. III. *C. cinereo-argentatus* (=*virginianus*); No. IV. *C. zerda*; No. V. *C. caama*; No. VI. *C. bengalensis*; No. VII. *C. corsac*; No. VIII. *C. velox* (the measurements taken from Dr. Baird's figure of the skull of this species); No. IX. *C. niloticus*; No. X. *C. lagopus*; No. XI. *C. fulvus*; No. XII. *C. vulpes*; No. XIII. *C. argentatus*.]

This is shown very clearly by the table of measurements on the preceding page of thirteen specimens belonging to twelve species of Alopecoids.

Thus *C. caama*, *C. bengalensis*, *C. corsac*, and *C. velox* appear to be mere local varieties of a small Alopecoid form answering pretty nearly to the Jackals in the Thooid series, and occupying the southernmost part of the Alopecoid zone, from South Africa to Central America. The more differentiated Alopecoids, though largely co-existent with these, are preponderant in the north of the zone.

I can meet with no evidence of the existence of any true Alopecoid in South America, which appears to be the head-quarters of the lower Thooids.

Among these, *C. vetulus* has the least modified dentition, and in this respect corresponds with *C. littoralis* among the Foxes. This species is figured and fully described by Burmeister. The skull has a low median sagittal crest; and the ramus of the mandible is slender and non-lobate. In the one imperfect cranium which I have seen (from which the measurements in Table XIII. are given) the length of the sectorial and first molar in the upper jaw is the same, and does not exceed 17 per cent. of the basicranial axis. The length of the lower sectorial is rather less than 23 per cent. The crown of the upper sectorial or fourth præmolar is broadly triangular (breadth in front 5·5 millims. to length 7 millims.), on account of the great size of its internal cusp, and resembles that of *Otocyon*. The inner anterior cusp of the lower sectorial is lower than the outer; but a line drawn through both is almost transverse to the axis of the tooth, the heel of which is very stout.

In Brazil, in Demerara, and in Guiana the canine animals which have been named *Canis cancrivorus*, *C. fulvipes*, *C. brasiliensis*, *C. rudis*, and that to which I have referred above as *C. azaræ* (a) occur. The crania belonging to the first four which have come under my observation are, for the most part, rather larger than that of the last, have a less-marked subangular lobe and slightly larger sectorial teeth; but there is no sharp line of demarcation between the two sets, and I regard them all as local varieties of *C. cancrivorus*. Moreover, in those forms, such as *C. rudis*, in which the skull is largest, the approximation to *Canis azaræ* (the most widely distributed of the South-American Canidæ) is so close, that I cannot separate the two by any osteological or dental characters.

Canis magellanicus presents the same sort of relation to *C. cancrivorus* as *C. simensis*, in the Old World, bears to *C. aureus* and *C. anthus*. The size of the body, and notably of the jaws, has

TABLE XIII.—*Cranial and Dental Measurements of South-American* Thooids.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	XV.	XVI.	XVII.	XVIII.
Total length	—	116	132	—	—	124	125	130	119	142	—	187	177	215	160	166	180	174
Length of palate	48	57	65	—	—	62	61	66	59	72	64	92	—	108	84	84	92	89
Breadth „	29	36	38	—	—	40	39	39	39	41	38	48	—	60	55	53	50	55
Length of basicranial axis..	42	44	47	—	—	43	49	47	44	48	50	60	61	66	57	56	58	57
„ $\underline{pm. 4}$	7	10	11	11·2	12	11·5	12	12	12	12·5	14	15	15·5	18	18	17	18	19
„ $\underline{m. 1}$	7	8	10	8·5	9·5	9	10	10	10·5	9	10	10	9·5	15	12	11	11·5	12·5
Breadth „	8	10	—	—	—	11	11	—	—	11	—	12	—	15·5	14·5	14	14	14·5
Length of $\underline{m. 2}$	5	5	6	5·7	7	6	6	6	7	5	6	6·5	6·3	10	6·5	5·5	7	6·5
Breadth „	6·5	7·5	—	—	—	7·3	7·5	—	—	7	—	10	—	12	9	8	10	8
Length of $\overline{m. 1}$	9·5	12·5	14	13·2	14	—	14	13·5	14·2	14·3	15	16	16	21·5	19	19·5	19·5	
„ $\overline{m. 2}$	6·5	6·5	7·5	7·2	8	—	7·7	8	8·5	7·5	8	—	8·7	11	8·5	8·5	8·7	
„ $\overline{m. 3}$	3	3·7	4	4	4·5	—	4	4·5	—	3·5	4·5	—	3·2	5·5	4	4	4·5	
„ $\overline{m. 4}$	—	—	2	2·5	—	—	—	—	—	—	—	—	2·5					

[No. I. *C. vetulus*; No. II. *C. azaræ* (a); Nos. III., IV., and V. *C. cancrivorus*; No. VI. *C. cancrivorus*, referred to above; No. VII. *C. fulvipes*; Nos. VIII. and IX. *C. rudis*; No. X. *C. azaræ*; described above; No. XI. *C. azaræ*; No. XII. *C. magellanicus*; No. XIII. *C. magellanicus*; No. XIV. *C. jubatus*; No. XV. *C. antarcticus*; No. XVI. *C. antarcticus*; No. XVII. *C. latrans*; No. XVIII. *C. antarcticus*, skull without the mandible. The measurements of a specimen of *C. latrans* are given here to show the extreme closeness of the relation between the "Prairie-Wolf" and its southern analogue.]

increased without any corresponding enlargement of the teeth (Table XIII.). In the large relative size of the upper molars, *Canis jubatus* adheres to the same type; while *C. antarcticus*, on the other hand, presents the closest approximation to some specimens of *C. latrans* (Table XIII.).

From the range of variation of *C. cancrivorus*, it can hardly be doubted that the examination of more extensive materials will prove the existence of an uninterrupted series of gradations from *C. vetulus* to *C. antarcticus* and *C. jubatus.* Burmeister[1] remarks that *Canis cancrivorus*, *C. fulvicaudus*, and *C. vetulus* are distinguished by the relative shortness of their jaws from *C. azaræ*, *C. griseus*, and

FIG. 15.—Side view of the skull of *Icticyon venaticus*: ⅔ nat. size.

C. magellanicus; but, so far as the measurements of his figures of the teeth permit me to form a judgment, *C. griseus* differs in no respect from some specimens of *C. cancrivorus.* With a shorter skull, Burmeister's specimen of *C. magellanicus* has larger sectorial teeth than either of the specimens I have seen.

In the lower jaws of two specimens of *C. cancrivorus*, and in one of *C. magellanicus*, in the British Museum, there is a well-formed though small fourth molar; and in a third specimen of *C. cancrivorus* there is a curious abnormal structure, consisting of a bunch of five

[1] Erläuterungen zur Fauna Brasiliens, p. 46.

minute crowns of teeth (whether united by their roots or not cannot be made out without injuring the specimen) in the place of the fourth lower molar on the right side.

Van der Hoeven [1] has described and figured a skull with a third upper molar on both sides, which he ascribes to *C. azaræ*, but which, according to Burmeister, belongs to *C. cancrivorus*.

In *C. cancrivorus*, therefore, the persistence of $\overline{m.4}$ seems to be a common occurrence, while $\underline{m.3}$ is found occasionally. Thus it would appear that we have under our eyes, in this species, another stage in the modification of the primitive dentition of the Canidæ, which, as

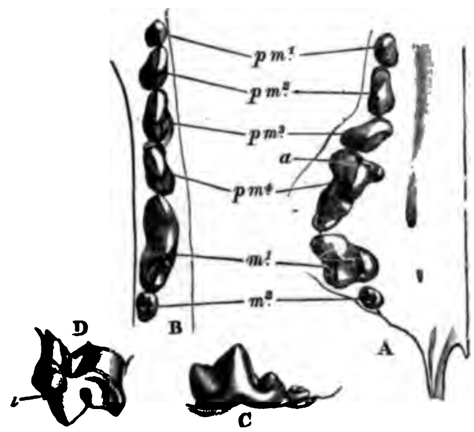


FIG. 16.—Upper (A) and lower (B) cheek-teeth of *Icticyon venaticus*; C, the right lower sectorial and second molar, from within; D, the right upper sectorial, from within; *a* the accessory cusp; the inner anterior cusp is not sufficiently well defined.

we have seen, has commenced even in *Otocyon*. And I think there can be no reasonable doubt that the occasional appearance of an extra molar in domestic Dogs is not a monstrosity, but a reversion to the earlier and more complete dentition of the primitive stock of the Canidæ.

In *Icticyon* the dentition is modified in the opposite direction, by the suppression of $\overline{m.3}$ and the reduction of $\underline{m.2}$. Indeed this tooth was supposed to be absent altogether, until Professor Flower recently observed it in a specimen which has already been the subject of a communication to the Society.

I am greatly obliged to the President for enabling me to give a figure of the skull (fig. 15) and teeth (fig. 16) of the specimen in question, which, though not quite fully adult, has the complete permanent dentition.

[1] "Over het geschlacht *Icticyon* van Lund," Verhandelingen der Koninklijke Akademie van Wetenschappen, Amsterdam, iii. 1856.

In the following table of measurements I add those of an imperfect skull in the British Museum.

TABLE XIV.—*Cranial and Dental Measurements of* Icticyon venaticus.

	I.	II.
Total length	118	
Length of palate	56	59
Breadth "	40	41
Length of basicranial axis	52	
" $\underline{\text{pm. 4}}$	11·5	13
" $\underline{\text{m. 1}}$	7	8
Breadth "	7	8
Length of $\underline{\text{m. 2}}$	3	
Breadth "	3	
Length of $\overline{\text{m. 1}}$	13	14·5
" $\overline{\text{m. 2}}$	4	5

In the British Museum specimen (No. II.) $\underline{\text{m. 2}}$ is absent, and there is no trace of any alveolus for it.

In absolute length, the skull No. I. (fig. 15, p. 434) comes very near *C. cancrivorus* (Table XIII. No. VI.), but differs from this in the relative length of the basicranial axis and shortness of the palate. It is a peculiarity of *Icticyon* which I have not observed in any other canine animal, that the upper and lateral margins of the occipital foramen are produced in such a manner as to give rise to a tubular prolongation which projects considerably beyond the occipital spine (fig. 15). Hence the total length given in Table XIV. is measured from the upper edge of this prolongation to the præmaxillary symphysis. The nasal bones are short and broad, and do not extend quite so far back as the fronto-maxillary suture. The glabellar region is evenly arched from side to side; and the postorbital processes are but slightly prominent; Burmeister's figure, however, shows that these become larger with age. The frontal sinuses are but slightly developed backwards; and this, judging by the marked constriction behind the postorbital processes in older skulls, appears to be the case even in old specimens.

The skull figured presents a narrow sagittal area, and the sagittal crest is undeveloped; but this feature also depends on the youth of the animal. In the large size of the paroccipital and mastoid processes, *Icticyon* resembles the larger Thooids of the Old World rather than its North-American congeners. The characters of the base of the skull are completely canine. The palate is wider in front than in *C. cancrivorus*. Posteriorly it is somewhat more prolonged and narrowed towards the nasal passage than usual; but a good deal

TABLE XV.—*Cranial and Dental Measurements of North American* Thooids.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
Total length	180	—	172	180	190	192	190	205	216	265
Length of palate	92	84	84	91	93	92	95	98	108	129
Breadth	50·5	49	52	54	55	54	54	63	67	79
Length of basicranial axis	58	—	52	59	59	57	61	69	73	85
,, $\underline{pm.}$	18	19	19	20	20·5	20	21	19·2	21	27
,, $\underline{m.1}$	11·5	12	12	13·5	12	12	13	12	14·5	18
Breadth ,,	14	14	14·5	15·5	14·5	15·5	15·5	15·5	16·5	21·5
Length of $\underline{m.2}$	7	6·8	6·5	8	7·5	7	7	6·5	8	9
Breadth ,,	10	9·5	10	10	10·5	11	11	10	11	13
Length of $\overline{m.1}$	19·5	20	21	22·5	21	21	21·5	22·5	24	30
,, $\overline{m.2}$	8·7	9	9	10	9·5	9	10	8·5	10	13
,, $\overline{m.3}$	4·5	4	4	5	4	4	5·5	4·5	6	6

of the peculiarity of appearance of this part of the skull of *Icticyon* arises from the small size of the hindermost molars.

The tympanic bullæ are not evenly arched as is usual in the smaller Thooids; but the outer is separated from the inner moiety of the convex surface by a well-defined oblique ridge. The rami of the mandibles are ankylosed together throughout the long symphysis, which measures 27 millims. This ankylosis has also taken place in the second specimen; and I am not aware that it occurs in any other of the Canidæ. The angle of the mandible is thick, short, and not produced inwards. Its lower edge is straight, and passes so abruptly into the convexity which follows, that the jaw presents, as it were, the next remove from the lobate condition beyond that of *C. fulvipes* (fig. 9, C, p. 419).

The upper incisors have the ordinary canine characters; and the large outer incisor is close to the second. The canines are very strong; and the first three præmolars are thick. Although the fourth præmolar has a length of only 11·5 millims., it is 7 millims. thick in front. The inner cusp, however, is very small. In both specimens a small but distinct cusp is developed from the anterior margin of the anterior blade-like cusp of this tooth. This is an unusual feature in the upper sectorial tooth of canine animals; and I am the more careful to draw attention to its existence, as, while Lund had mentioned the fact, Burmeister expressly denies it:—"Der Fleischzahn des Oberkiefers ist ganz Hundeartig, d. h. der innere Nebenhöcker sehr klein; und die äussere Höckerreihe ohne den dritten vordern Höcker, welcher den Viverrinen zusteht" (*l.c.*, p. 9). It is to be presumed therefore that this minute cusp was absent in Burmeister's specimen.[1]

The crown of the first upper molar is triangular and comparatively narrow, in consequence of the reduction of the cingulum and the disappearance of the posterior inner cusp. The crown of the minute second molar is nearly circular, with a median depression separating rudimentary outer and inner cusps (fig. 16, A). The lower sectorial presents peculiarities already noted by previous observers. Thus, the inner anterior cusp has altogether disappeared, the heel is very short, and the inner posterior cusp has also vanished. The second lower molar is very like the upper, its crown presenting a median depression bounded outside and inside by minute cusps, of which the inner is the lower (fig. 16, B, p. 435).

[1] Similar but better-developed anterior basal cusps occur in the upper sectorial of *Otocyon*, and occasionally in other Canidæ, as *C. anthus*, *C. zerda*, and *C. bengalensis*. Hence no great taxonomic importance can be assigned to this character.

Thus the dentition of *Icticyon* is far more different from that of the ordinary Canidæ than that of any other known canine animal, whether recent or extinct, except *Otocyon*, standing in some respects at the opposite pole to the latter.

In all other points, *Icticyon* is not only, as Lund proved, unmistakably a member of the canine group, but it is so closely allied to the other North-American Thooids, that I can only regard it as a modification of the *Canis cancrivorus* type, analogous to that which, among the Old-World Jackals, has given rise to *Cyon*, but carried a step further.

In North America the Thooid division is represented only by such macrodont forms as *C. latrans* and *C. lupus* (*occidentalis*).

The foregoing Table (XV.) gives the measurements of seven crania of *Canis latrans* in the British Museum and in the Museum of the Royal College of Surgeons. The exact locality of No. I. is unknown; No. II. is from Hudson's Bay; No. III. from Grand Isle, Platte Rock; No. IV. from Medicine Creek, Nebraska; No. V. from Fort Colville; No. VI. from Fort Kearney; and No. VII. from Columbia River. They therefore cover almost the whole extent of North America in longitude, and, as might be expected, exhibit a considerable range of variation, though probably less than a larger series would show.[1] But, as they are, I must confess myself unable to find any important break in the series of gradations of cranial and dental structure between *Canis latrans* and *C. antarcticus*, on the one hand (see Table XIII.), and *C. latrans* and *C. occidentalis* (Table XV., VIII., IX., X.) on the other. Moreover, considering that only two sets of measurements of *C. magellanicus* are given, it is not unreasonable to expect that, with a larger series of this form, all the American Thooids, so far as their dental and cranial characters are concerned, would be susceptible of arrangement in a continuous series of almost imperceptible modifications. I may further remark that I can discern no difference of the slightest importance between skulls of *C. latrans* and those of some of our domestic Dogs.[2]

Of the three skulls of *Canis occidentalis* (Table XV. Nos. VIII., IX., X.), No. X. is a very large typical Wolf-skull, nowise distinguishable from the most characteristic examples of the Old-World Wolves. Nos. VII. and VIII., on the other hand, have teeth not at

[1] Baird's observations ("Report," under *Canis*) point to an extraordinary amount of local variation in *C. occidentalis* and *C. latrans*.

[2] The close resemblance of *C. latrans* to certain domestic Dogs of the Old World has already been noted by Jeitteles and Coues. See the former writer's excellent essay "Die Stammväter unserer Hunde-Rassen," 1877.

all, or but little, larger than those of some specimens of *C. latrans*, from which they differ chiefly in the greater width of the palate and total length of the skull. Moreover, in these skulls the facial line, instead of being nearly straight or even slightly convex, as is usual in Wolves, Jackals, and domestic Dogs of the Greyhound type, is as concave as in the skulls of many Newfoundland Dogs and Mastiffs, to which they present striking resemblances.

If we now leave the New World for the Old, travelling westward, it is a very interesting fact that in Japan, in the Amur basin, and in North China we meet with a form of canine animal which has been made the type of a distinct genus, *Nyctereutes*, but which is essentially a low Thooid of the South-American type. This is the *Canis procyonoides*,[1] of the external characters, the skeleton, and dentition of which a full account has been given by Schrenck (" Reisen und Forschungen im Amurlande," Band i. 1858).

TABLE XVI.—*Cranial and Dental Measurements of* Canis procyonoides.

	I.	II.	III.	IV.
Total length	115	107	96	—
Length of palate	57	55	49	54
Breadth " . . .	34	33·5	38	34
Length of basicranial axis	39	—	39	41
" $\underline{pm. 4}$	9·7	10	10	11
" $\underline{m. 1}$	8	8	8·5	9
Breadth "	8·2	8·6	—	9
Length of $\underline{m. 2}$	5	5	5	5
Breadth "	6	6		
Length of $\overline{m. 1}$	11	12	12	12
" $\overline{m. 2}$	6	6	6	6·5
" $\overline{m. 3}$	3	—	—	3

This is made manifest by the comparison of the measurements of the skulls I., II., III., IV. in the preceding Table (of which No. II. is from " North China," while the rest are Japanese) with those of *Canis azaræ* (a) given in Table XIII.

Nos. I. and II. are adult skulls having a narrow lyrate sagittal area, and curiously similar to *Otocyon* in the elongation of the jaws and the marked lobation of the mandible. The outer incisor above is separated from the others by a distinct interval ; and the bony palate extends for 2–5 millims. behind the level of the hindermost

[1] The specific name appears to me to be as little applicable as the generic distinction of "*Nyctereutes*" is justifiable. Beyond a superficial external resemblance, there is nothing of the Raccoon about this animal.

TABLE XVII.—*Cranial and Dental Measurements of* Cyon.

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
Total length	163	—	167	164	184	177	—	174	183
Length of palate	77	82	77	82	85	85	98	85	90
Breadth "	55	57	59	60	61	61	68	65	65
Length of basicranial axis	—	—	60	60	68	67	69	65	61
" $\underline{pm.\,4}$	19	19	19	20	20.5	20.5	20.5	22	21.2
" $\underline{m.\,1}$	12.5	12	13	12	13	13	13	13.5	15
Breadth "	12.5	12	14	13	13.5	13.5	14.5	14	15
Length of $\underline{m.\,2}$	6	4.5	5.3	—	5.5	5	5	5	7
Bread h "	8.5	5	8	—	7.5	8	8	7.3	10
Length of $\overline{m.\,1}$	20	20	21	21	21	21.5	21.5	22.5	23
" $\overline{m.\,2}$	7.5	7	8	8	7	7	9	8	9

[*C. sumatrensis*, No. I., is from Sumatra; No. II. from Malacca; *C. primævus*, Nos. III. and V., from Sikkin; *C. dukhuensis*, No. IV., from Central India; No. VI. from Cashmere; No. VII. from Cuttack; No. VIII. from Nepal; *C. alpinus*, No. IX., from the Altai.]

molars. No. III. is young, the permanent teeth not having completely emerged.

The Japanese *C. hodophylax*, of which there is a fine specimen now living in the Gardens, appears to be simply a small form of Wolf; but in the absence of any accessible skulls of this form or of *C. nippon*, I refrain from giving any definite opinion about them. All the Asiatic Thooids, north of the Altai, appear to be mere varieties of *C. lupus*. But in the Altai range itself, in the upper basins of the Jenessei and the Lena, and as far eastward as the shores of the Sea of Ochotsk, the *Canis alpinus* makes its appearance (Schrenck, *l.c.*, pp. 48–50).

This species, *C. primævus*, *C. dukhunensis*, and *C. sumatrensis*, have been separated as a distinct genus, *Cyon* (*Cuon*, Hodgson), on account of the constant absence of $_{m.3}$. They agree, not only in this respect,[1] but in the breadth of the jaws and, very generally, in a marked convexity of the facial line. In this respect they depart from the ordinary Wolves and Jackals in the opposite direction to some Wolves and to the majority of the domestic Dogs, in which this contour tends to become strongly concave.

The Table of measurements on preceding page of nine skulls shows the close affinity of the forms associated under *Cyon*.

In none of these skulls was a trace either of the hindermost lower molar or of its alveolus to be seen. Jerdon states that *C. primævus* "is common in Ceylon, where it is called the Dhole by some, by which name it has been treated of by Hamilton Smith and other writers; and it is found all over the jungles of Assam, Burmah, and the Malayan peninsula," which is in contradiction to the commonly received opinion that there are no wild Dogs in Assam and Burmah. According to S. Müller, the same species is found in Borneo.

The distribution of this group over an area which covers nearly 60 degrees of latitude and about as much of longitude in Eastern and Southern Asia is very remarkable, when taken in conjunction with the fact that the proper Jackals, although co-existent with *Cyon* in Hindostan, are absent over the rest of the *Cyon* area, except perhaps in Burmah; while, to the westward of Hindostan, *Cyon*, so far as is known, is absent in the vast area inhabited by the Jackals. For the species united under *Cyon* appear to me to be nothing but large and slightly modified forms of the Jackal type, which thus seems to have become somewhat specialized at the eastern extremity of its area of distribution.

[1] Van der Hoeven (*l.c.*) mentions that he found $\overline{m.3}$ present in one specimen of *C. rutilans* out of six examined.

TABLE XVIII.—*Cranial and Dental Measurements of Jackals.*

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.	XIII.	XIV.	XV.	XVI.	XVII.	XVIII.	XIX.
Total length	136	154	140	145	159	150	165	147	157	150	175	168	168	150	165	—	203	155	155
Length of palate . . .	66	76	72	70	75	71	78	70	77	74	85	84	83	76	81	87	104	82	79
Breadth	45	51	48	47	51	50	54	50	52	54	57	54	53	53	53	54	53	45	48
Length of basicranial axis	51	55	—	52	—	55	—	49	56	59	—	56	59	53	53	—	65	54	51
Length of $\underline{pm.\,4}$	15	15	15·5	15·5	16	16	17	17	17	17	17	18	19	17	18	17	16·5	14·5	19
„ $\underline{m.\,1}$	12	—	13	11*	11·5	12	13	12	12	13	14	13	12	12	12	13	13	11	12
Breadth „	12	—	13	12·5	13	12	14·5	13·5	12	14	15	13	14	14	15	15	13	12·5	14·5
Length of $\underline{m.\,2}$	6	—	6	6	7	6	7	6	5	7	7	7	7	7	6·5	7·5	8·5	7	7·5
Breadth „	8	—	9	9	10·5	9	9	9·5	7	10	11	9	10	10	11	12	10	9	10
Length of $\overline{m.\,1}$	19	19	19	18	18	19	20	19	19·5	18	21	19	20	19	19	20	19·5	17	20
„ $\overline{m.\,1}$	8	8	8	8	9	8·5	9	8	8	10	9·5	9	9	9	8·5	10	10·5	9	9
„ $\overline{m.\,3}$	4	4	4	3·5	4·3	4	4	4	5·5	—	4	4	4	—	—	5	4·2	5	5

[Nos. I. to XIII., *C. aureus*, from India ; Nos. XIV. to XVI., *C. anthus*, from North Africa ; No. XVII., *C. sinensis*, from Abyssinia ; No. XVIII., *C. lateralis*, from the Gaboon ; No. XIX., *C. mesomelas*, from South Africa.]

I have already referred to the variability of *Canis aureus*; and the amount of variation exhibited by that species will become still more apparent by an inspection of Table on page 443 of measurements of the skulls of thirteen specimens of *Canis aureus* from India. From this it appears that the skull of this species may vary in absolute length 28 per cent., in the length of the palate by nearly 30 per cent., in its width by more than 25 per cent., in the length of the basicranial axis by about 20 per cent., in the length of $\underline{pm.4}$ rather more than 25 per cent., in the length of $\overline{m.1}$ about 11 per cent.

If the measurements of *C. anthus*, *C. lateralis*, *C. simensis*, and *C. mesomelas*, given in the same table, are compared with those of *C. aureus*, it is obvious that the great majority fall into place somewhere in the series of *C. aureus*; and the only notable difference is in *C. simensis*, in which there is a remarkable elongation of the palate. But this is exactly that part of the skull which varies most in *C. aureus*; and the difference in length between the longest and shortest palate in this species, 19 millims., is exactly the same as that between the longest palate of *C. aureus* and that of *C. simensis*. I do not doubt that a larger number of specimens of *C. anthus* and of *C. simensis* would afford a complete series of intermediate forms between them and the Common Jackals.

Just as, at the eastern extremity of the Jackal area, the large *Cyon*-form with specially modified dentition is met with, so at its western extremity, in South Africa, the large *Lycaon*-form, with specially modified fore feet, occurs. In the breadth of the præmolar region of the upper jaw, and in a more or less marked convexity of the facial contour, *Lycaon* strongly reminds one of *Cyon*; but the dentition is complete, stronger, and more wolf-like, and the edges of the hinder præmolars are more deeply lobed.

TABLE XIX.—*Cranial and Dental Measurements of* Lycaon.

	I.	II.	III.	IV.	V.
Total length	185	194	203	—	250
Length of palate	88	91	100	98	100
Breadth ,, ...	76	73	69	71	74
Length of basicranial axis	63	69	68	71	69
,, $\underline{pm.4}$	20	20	20	20·5	21
,, $\underline{m.1}$	15	15	15	16·5	16
Breadth ,, ...	15·5	15·5	16	—	16·5
Length of $\underline{m.2}$	7	6	7	7·5	7·5
Breadth ,, ...	9	8	10·5	—	10
Length of $\overline{m.1}$	23·5	24	24·5	25	25
,, $\overline{m.2}$	9·5	10	9	9	11
,, $\overline{m.3}$	—	4	4·5	4·2	5

TABLE XX.—*Cranial and Dental Measurements of Wolves of the Old World.*

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Total length	215	223	234	236	240	240	250	237
Length of palate	109	102	110	111	109	119	111	116
Breadth ,,	72	71	72	70	73	77	82	79
Length of basicranial axis	71	62	74	—	71	77	78	75
,, $\underline{pm.\,4}$	21·5	22	23·5	24	24	25	28	29
,, $\underline{m.\,1}$	15	15·5	16	16	16·5	16	17	17
Breadth ,,	16·5	17	16·5	18	19·5	17	20	20
Length of $\underline{m.\,2}$	8	8·5	8	8	9	8	9	9
Breadth ,,	10·5	13	10·5	12	13	11	13·5	13
Length of $\overline{m.\,1}$	24·5	26·5	25·5	28·5	28	28·5	30	30
,, $\overline{m.\,2}$	10	10·5	11·5	12	12	11	12	12·5
,, $\overline{m.\,3}$	—	5·5	5·5	—	6	4	5	5·5

[No. I., *C. pallipes*, from India ; No. II., *C. lupus*, from Belgium ; No. III., *C. pallipes*, from India ; No. IV., *C. chanco*, from Thibet ; No. V., *C. lupus*, from Russia ; No. VI., *C. laniger*, from Thibet ; Nos. VII. and VIII., *C. lupus*, European, but the locality not certainly known.]

The Indian Wolf, *Lupus pallipes*, more nearly approaches the Jackals than any other Old-World Wolf I have seen. But only two skulls of this species have as yet come into my hands; and though they differ considerably, the chances are greatly against their representing the extremes of variation of the species. When the Canidæ of Turkestan are better known than at present, I have little doubt that the inconsiderable break between the Old-World Jackals and Wolves will be filled up.

It is obvious that the range of variation of the Eastern is as great as that of the Western Wolves (Table XX.); and I conceive that *C. pallipes*, *C. chanco*, and *C. laniger* must be regarded as mere local varieties of *C. lupus*, inasmuch as the table shows that the European Wolf (Nos. II., V., VII., VIII.) includes within its range of variation all the cranial differences presented by these so-called species.

13. The palæontological history of the Canidæ is, at present, very imperfect; but sufficient has been ascertained to enable us to obtain a general conception of the phylogeny of the group.

There is no question that Thooids and Alopecoids similar to those which exist at present inhabited Europe during the Quaternary epoch. Remains of the Dingo have been found in Australian deposits of apparently the same age; and the explorations of Lund in the Brazilian caves have demonstrated the existence of several forms of Canidæ of the existing South-American types—among the rest, of *Icticyon*, with which I conceive Lund's *Speothos* must be merged.

The *Palæocyon* of Lund, a large wolf-like animal with forty-two teeth, but with the second upper molar very small and with the inner cusp of both the upper and the lower sectorials (which measure not less than 28 millims. in length) obsolete, has no representative in the existing fauna. This fact is the more interesting, as the dentition of *Palæocyon*, in some respects, presents a more thoroughly carnivorous aspect than that of the Old-World Wolves.

Information respecting the Pliocene Canidæ is scanty. One of the best-known forms is the *Canis borbonidus* (*C. megamastoides* of Pomel), briefly described and figured by Gervais in the "Paléontologie Française" (ed. 2, p. 213, pl. xxvii. fig. 7). An almost entire skeleton was obtained from the Pliocene of Cerdé near Issoire. The skull is 150 millims. long; and Gervais justly observes that the ramus of the mandible resembles that of *C. cancrivorus*. From the figure I judge that the teeth were no less similar to those of this

species. The humerus has an intercondyloid but no supracondyloid perforation; and the digits are five in front and four behind.

Opinions differ as to whether the deposits of Œningen should be reckoned Lower Pliocene or Upper Miocene. The skull of the famous fossil Fox of Œningen, originally described by Mantell, and subsequently made the type of a new genus, *Galecynus*, by Professor Owen, is unfortunately not in a sufficiently good state of preservation for the determination of the question whether it belongs to the Alopecoid or to the Thooid series. In its cranial and dental measurements it agrees with surprising closeness with the common Fox; and this correspondence extends even to the form and dimensions of the left upper sectorial tooth, which I have recently found could be readily exposed for about half its length in the specimen preserved in the Geological Society's Museum. There is, however, a rather stronger indication of a secondary cusp on the anterior part of the base of the blade of this tooth than is usual in the Foxes. At present I fail to see any sufficient ground for placing this animal in a distinct genus from the Foxes. Considering the known amount of variation in the pollex of different Canidæ, its slightly greater proportional length in the Œningen skeleton, though an interesting fact in itself, can hardly be regarded as of much systematic importance.

Much light has recently been thrown upon the palæontological history of the Canidæ by M. Filhol's[1] important researches upon the fossils of the phosphoritic deposits of Upper Eocene age in France, and especially upon the abundant remains of the genus *Cynodictis*. Of these "viverrine Dogs," as M. Filhol calls them, he distinguishes no fewer than seventeen varieties, which shade off, on the one hand, into true Viverridæ, and, on the other hand, into the Amphicyonidæ.

M. Filhol has so fully described and so well figured examples of a large suite of specimens of the different forms of *Cynodictis*, that it is possible for those who have not enjoyed the opportunity of examining his materials to form an independent judgment as to the conclusions which may be drawn from them; and on one or two points I venture to dissent from his views.

Thus, in treating of *Canis filholi*, M. Filhol observes:—

"Je ne crois pas que ce soit là un *Canis* vrai, car le tubercule interne de la carnassière est beaucoup trop développé; il est fort

[1] "Recherches sur les phosphorites de Quercy," Bibliothèque de l'École des Hautes Études, xv. et xvi. 1876, 1877.

élevé et se réunit par son bord antérieur au bord postérieur de la pointe antérieure ; la portion moyenne de la face interne de la pointe principale n'est pas visible en dedans comme sur les Chiens vrais, elle est marquée à sa base par l'union des deux autres pointes." [1] . . . . "Je serais assez porté à penser que le *Canis filholi* doit rentrer dans le groupe du *Cynodictis cayluxi*, auquel le rattache la forme de la carnassière du *Cynodictis intermedius*. Il indique certainement une tendance des *Cynodictis* à prendre les caractères des Canidés, mais l'ensemble de ses caractères est trop viverrien encore pour qu'on puisse le placer parmi les *Canis*. La même observation doit être faite pour le *Cynodictis crassidens*. Ces types sont excessivement intéressants, car ils paraisaient peut-être indiquer par la dégradation successive des caractères de la carnassière l'origine ancienne de nos Chiens."

But the characters of the tooth to which M. Filhol refers cannot be regarded as sufficient to differentiate *Cynodictis* from the true *Canidæ*, when we have in *Otocyon* (fig. 13, C, p. 426) a lower sectorial which may be described in the same terms. In fact, apart from the number of the teeth, the dentition of *Otocyon* departs more widely from that of the more differentiated Canidæ than that of *Cynodictis* does, the teeth of the latter taking a place alongside of those of the lower Thooids and Alopecoids.

After describing the skull of *Cynodictis boriei*, M. Filhol remarks :— "Il n'y a rien dans le groupement des diverses parties dont j'ai successivement indiqué la position qui permette une comparaison avec les différents groupes de nos Carnivores. La base du crâne des Ursidés, des Canidés, des Viverridés, des Félidés, des Hyænidés, des Mustélidés, est tout-à-fait différente ; celle des Marsupiaux l'est également" (*l.c.*, t. xv. p. 74).

Without inspection of the specimens on which M. Filhol bases this opinion, it is hazardous to traverse it ; but I confess his detailed description and excellent figures lead me to form a different conclusion, and to think that, in cranial characters, *Cynodictis* nearly approaches the South-American Thooids ; and especially *Icticyon*, in the proportions of the face and skull.

In the actual measurements of the palate and of the teeth, *Cynodictis* comes extraordinarily near to certain living South-American forms. Thus, *C. leptorhynchus* is very like *C. vetulus* while *Cynodictis gryei* almost as closely approaches *C. azaræ*—the chief difference, in the latter case, being the less transverse diameter of the sectorial and of the two molars of the upper jaw in *C. azaræ*.

[1] *Loc. cit.*, tome xvi. p. 319.

TABLE XXI.—*Cranial and Dental Measurements of* Cynodictis *and* Canis.

	I.	II.	III.	IV.	V.
Length of palate	42	48	79	72	—
Breadth „	29	29	39	41	—
Length of $\underline{\text{pm. 4}}$	8	7	13	12·5	14
Breadth „	5	5·5	9	6	10
Length of $\underline{\text{m. 1}}$	6	7	—	9·3	11
Breadth „	7·5	8	—	11	15
Length of $\underline{\text{m. 2}}$	4	5	6·5	6	8
Breadth „	6·5	6·5	9	7	9·5
Length of $\overline{\text{m. 1}}$	7	9·5	—	14·5	13·5
„ $\overline{\text{m. 2}}$	4	6·5	—	7·5	—
„ $\overline{\text{m. 3}}$	3	3	—	4	—

[No. I. *Cynodictis leptorhynchus*; No. II. *Canis vetulus*; No. III. *Cynodictis gryei*; No. IV. *Canis azaræ*; No. V. *Cynodictis boriei*. The measurements are partly given by M. Filhol and partly taken from his figures.]

The skull of *Cynodictis boriei* is as large as that of an ordinary European Wolf, so that the microdont character is very striking, while the great thickness of the upper sectorial and the large size of the upper molar brings this form still nearer to *C. vetulus* than to *C. azaræ*.

Taking all the facts of the case into consideration, I am disposed not only to agree with the conclusion to which M. Filhol's remarks tend, that *Cynodictis* lies in the direct line of ancestry of the Canidæ, but to suppose that, in skull and teeth, it represents pretty closely the stock from which the branch of the Viverridæ has diverged, subsequently to give rise to the Felidæ and Hyænidæ.

On the other hand, as M. Filhol points out, certain forms of *Cynodictis* closely approach *Amphicyon*, a genus in which $\underline{\text{m. 3}}$, usually aborted in all the existing Thooid and Alopecoid Canidæ, is present, though much smaller than $\underline{\text{m. 2}}$ and evidently in course of suppression. In other respects, as in the shortness of $\overline{\text{pm. 4}}$ relatively to $\underline{\text{m. 1}}$, the large size of $\underline{\text{m. 2}}$ relatively to $\underline{\text{m. 1}}$, and of $\overline{\text{m. 2}}$ relatively to $\overline{\text{m. 1}}$, the dentition of *Amphicyon* repeats the general characters of that of *Cynodictis*.

None of the varieties of *Cynodictis* or of *Amphicyon* exhibits a distinctly lobate form of mandible; nor, so far as I am aware, has any specimen of the latter genus been discovered with more than three molars above and below. Hence, if I am right in supposing that in the dentition of *Otocyon* we have a representation of the

number and the kinds of teeth which existed in the earliest ancestors of the Canidæ, and that the lobate mandible is similarly inherited from them, it becomes necessary to seek, for the primitive forms of the Carnivora which probably stood in the same relation to *Amphicyon* as *Otocyon* does to *Canis* and *Vulpes*, in still older formations. Nothing is at present known of the Mammals of the Cretaceous epoch; and from the older Eocene the only forms which bear upon the present question are *Arctocyon*, *Pterodon*, and *Hyænodon*. Of the first too little is known to warrant speculation. With respect to the two latter, M. Filhol's observations have conclusively proved that they have as little to do with the Didelphia in dentition as in other respects; and he has described an interesting form, *Cynhyænodon*, the upper dentition of which approaches that of *Pterodon*, while its mandibular teeth present resemblances to those of *Cynodictis*.

I do not suppose, however, that *Pterodon* (and still less *Hyænodon*) lies in the direct line of ancestry of the Canidæ. On the contrary, they appear to constitute a peculiar branch of the stock of the Carnivora, having closer relations to the Insectivora than are possessed by modern Carnivores.

In fact, in *Centetes*, the molar teeth of both jaws increase in size from before backwards, and the patterns of their crowns are such that those of all the Carnivora may be readily derived from them. The trihedral prism which constitutes the chief part of the first upper molar of *Centetes* obviously answers to the triangular elevation on the crown of the corresponding tooth of *Otocyon*, which terminates in the two outer and the two inner cusps; and the main difference between the two is that the cingulum is larger and extends much nearer to the summits of the cusps in *Otocyon* than in *Centetes*.

In the mandibular teeth, again, the first molar of *Centetes* presents exactly the same number of cusps, disposed in the same way as in that of *Otocyon*, the difference between the two lying merely in the different proportions of the parts. The exact correspondence in plan of these teeth is the more interesting, since, in *Centetes*, it is easy to trace the progressive changes by which the simple and primitive character of the Mammalian cheek-tooth exhibited by the most anterior præmolar passes into the complex structure of the crowns of the posterior teeth.

This is particularly obvious in the lower cheek-teeth, in which the crown of the most anterior præmolar is simply tricuspidate, with the anterior and the posterior cusps very small and the apex of the

principal cusp simple. In the next præmolar the principal cusp appears cleft near its apex, in consequence of the development of a small secondary cusp on its inner side; the anterior cusp is higher and the posterior both higher and thicker. In the third præmolar, and in the molars, the anterior cusp is still higher; the secondary cusp is as large as that from which it is derived, so that it answers to the anterior internal cusp, while the former principal cusp takes the place of the anterior external cusp of the typical canine tooth. The posterior cusp, become very broad, and divided by a faint median depression, represents the posterior external and posterior internal cusps of the lower sectorial of the Dogs. A series of changes of just the same kind is observable in *Gymnura*; but the posterior cusps acquire a much greater size, and the molars take on a procyonoid character.

If the cheek-teeth of *Centetes*, *Gymnura*, *Otocyon*, and *Nasua* are placed side by side, it is easy to see that the first presents the least-modified condition of the pattern of the crowns of the molars common to the whole series. The reduction, or the less development, of the addition to the inner sides of the teeth, on the other hand, would give such crowns as those of *Pterodon* and *Hyænodon*.

The Insectivorous affinities of the dentition of the lower Carnivores harmonize very well with other peculiarities of the group.

The presence of a rudimentary clavicle and of a rudimentary hallux in the existing Canidæ leaves no reasonable doubt that they are descended from ancestors which possessed both in a complete state. And the suggestion is no less obvious that their digitigrade condition has resulted from the modification of a plantigrade form. Now we do not know whether any of the Eocene Canidæ possessed clavicles; but there is reason to believe that *Amphicyon* was plantigrade and pentadactyle.

M. Filhol has shown that *Cynhyænodon* had a brain more like that of an Insectivore than that of a Carnivore; and this fact is in accordance with a rule which now rests on a pretty broad basis of induction, that, in any given series of Mammals which is represented throughout the Tertiary series, the oldest forms had less highly developed brains than their modern representatives.

But, if the oldest Tertiary Carnivores were pentadactyle, plantigrade, claviculate, and had brains with relatively small cerebral hemispheres and large, completely exposed, cerebella, one may ask,

by what characters were they distinguishable from the Insectivora? and why may not *Hyænodon* and *Pterodon* be an extreme development of that type of the Insectivora which is at present represented by *Centetes*?

On the other hand, if the primitive stock of the terrestrial Carnivora was represented by a plantigrade, pentadactyle, claviculate form with the dentition and jaw-angle of *Otocyon* and provided with epipubes, we should be furnished with that which is at present wanting, namely a link between the monodelphous and the didelphous Mammalia. According to our present system of classification, such a mammal would be grouped among the Insectivora, or as a transitional form between them and the *Didelphia*; and I have long entertained the conviction that the primary stock of all the groups of the monodelphous Mammalia will be found to occupy this position.

14. It may be desirable to state in a summary form the principal conclusions to which the facts stated in the preceding pages appear to me to point.

I. The existing Canidæ exhibit a gradual series of modifications, in the form and size of their skulls and the number and characters of their teeth, from *Otocyon*, as the least-differentiated member of the group, to the Wolves, Lycaons, Cyons, and the Northern Foxes, as the most modified forms.

II. In the skull these modifications consist chiefly (*a*) in the increase of absolute size; (*b*) in the increase of the relative dimensions of the jaws, and particularly in the width of the palate; (*c*) in the persistence or disappearance of the sagittal area common to all young Canidæ, and the correlative development or absence of a sagittal crest; (*d*) in the diminution of the inflexion of the angular process of the mandible; (*e*) in the disappearance of the subangular lobe.

III. In the teeth, the most important modifications are the increase in the proportional size of the sectorials, accompanied by the relative diminution and, in some cases, suppression of the posterior molars. In *Otocyon*, $\underline{m.4}$ has usually disappeared. In *C. cancrivorus*, $\underline{m.4}$, $\underline{m.3}$, and $\overline{m.4}$ are most frequently suppressed; but $\overline{m.4}$ often remains, and $\underline{m.3}$ persists in one known case. In the great majority of the Canidæ, $\underline{m.4}$, $\underline{m.3}$, and $\overline{m.4}$ are normally suppressed, while $\overline{m.3}$ becomes relatively small, and, as a rule, disappears in *Cyon*. Finally, in the majority of examples of *Icticyon*, both $\underline{m.2}$ and $\overline{m.3}$ are wanting, and when $\underline{m.2}$ is present it is very small.

The gradation will be rendered more intelligible by placing the formulæ of the cheek-teeth under one another.

	Maxilla.		Mandible.	
	pm.	*m.*	*pm.*	*m.*
Otocyon:				
Fullest dentition observed . .	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4
Ordinary	1 2 3 4	1 2 3 *	1 2 3 4	1 2 3 4
C. cancrivorus:				
Fullest dentition observed . .	1 2 3 4	1 2 3 *	1 2 3 4	1 2 3 4
Ordinary	1 2 3 4	1 2 * *	1 2 3 4	1 2 3 *
Most Alopecoids and Thooids .	1 2 3 4	1 2 * *	1 2 3 4	1 2 3 *
Cyon	1 2 3 4	1 2 * *	1 2 3 4	1 2 * *
Icticyon:				
Fullest dentition observed . .	1 2 3 4	1 2 * *	1 2 3 4	1 2 * *
Ordinary	1 2 3 4	1 * * *	1 2 3 4	1 2 * *

In the individual teeth, the most important changes are the increase of the length in proportion to the breadth of the upper sectorial, and, in the lower sectorial, the change in the relative dimensions and position of the inner anterior cusp, which, from being on a level with the outer and higher than it in *Otocyon*, becomes smaller and shifts further and further backwards, eventually even disappearing, as in *Icticyon* and *Palæocyon*. The heel of this tooth also diminishes in proportion to its blade.

IV. All the known kinds of canine animals may be arranged in two series, starting from *Otocyon* as the nearest ally of the lowest member of each series.

It is probable that when a sufficient number of specimens of each species at present recognized has been examined, it will be found that the forms with least-modified skulls and teeth are connected by insensible gradations with those with most-modified skulls and teeth, and that no absolute line of demarcation can be drawn between one species and another in cranial and dental characters.

There is no evidence that any one of these species is infertile when crossed with any other. Such evidence as exists with respect to *C. cancrivorus*, the Jackal, Dog, and Wolf tends to the conclusion that species of approximately the same size are capable of fertile unions.

V. The taxonomy of the Canidæ, under these circumstances, is very much a matter of convention. I am disposed to think that the most convenient mode of representing the facts is to regard *Otocyon* and the Thooid and Alopecoid series respectively as genera, retaining for the two latter the old names of *Canis* and *Vulpes*.

In each of these genera a lower, a middle, and a higher section may be conveniently recognized, though they are hardly susceptible of strict definition.

Thus, in the genus *Vulpes*, Baird has separated *V. littoralis* and *V. cinereo-argentatus* under the name of *Urocyon*. The Corsacine Foxes, *V. zerda*, *V. caama*, *V. bengalensis*, and *V. velox*, may constitute another subgeneric section, and the most differentiated Foxes, such as *V. lagopus*, *V. fulvus*, and the rest, a third.

In the genus *Canis* we have, in like manner, as a lowest section the species of the *C. cancrivorus* and *C. vetulus* type (answering pretty much to the Aguarra Dogs of Hamilton Smith), the Sacaline section (*C. aureus*, *C. anthus*, *C. mesomelas*, *C. antarcticus*, *C. latrans*), and the Lupine section (*C. lupus* and all its varieties). *Icticyon*, *Lycaon*, and *Cyon* may probably be usefully retained as subgeneric names for the special modifications of the Thooid type which are denoted by them.

As for species, no one zoologist has ever yet agreed with the estimate of another as to what should be considered species and what local varieties among Wolves and Foxes; and, as there is no criterion by which the question can be decided, it is probable that such agreement never will be attained. The suggestion that it may be as well to give up the attempt to define species, and to content oneself with recording the varieties of pelage and stature which accompany a definable type of skeletal and dental structure in the geographical district in which the latter is indigenous, may be regarded as revolutionary; but I am inclined to think that sooner or later we shall have to adopt it.

VI. The most notable facts in the Distribution of the Canidæ are:—(1) the occurrence of the Corsacine Alopecoids and the Sacaline Thooids, side by side, from South Africa, through Central Asia, to India and North and South America; (2) the limitation of *Otocyon* to South Africa; (3) the limitation of Aguarine Thooids to South America and North-east Asia, including Japan; (4) the limitation of the most specialized Thooids, namely the Wolves and the ordinary Foxes, to the Northern hemisphere; (5) the exclusion of Foxes from South America; (6) the distribution of *Cyon*, which curiously resembles that of the Tiger.

If provinces of distribution were marked out by the Canidæ, they would by no means correspond with those generally recognized. There is nothing peculiar about the Australian dog, while the American continent contains within itself all the chief types of Canine animals, except *Otocyon*. The presence of this form, with its

ancient type of dentition, in South Africa is not improbably due to the fact that this region contains the remains of a very old Mammalian fauna.

VII. The morphological relations of the living Canidæ are such as to suggest that they result from the gradual accumulation of small variations in the general direction of increase of size and of differentiation of the teeth, superinduced upon a primitive stock which presented the full microdont dentition of *Otocyon*.

VIII. Though the palæontological history of the Canidæ is incomplete, the facts which are ascertained tend in the same direction In skull and dentition, the older Tertiary Canidæ either, as in the case of *Cynodictis*, resemble the less-differentiated Canidæ, or, as in *Amphicyon*, present a third upper molar, such as occasionally exists in *Canis cancrivorus*. But if, as I suppose, *Cynodictis* and *Amphicyon* were preceded by forms having four molars above and below, they have yet to be discovered, as no Eocene mammals with four molars, except Opossums, have as yet been brought to light.

IX. The primitive stock of the Dogs, for which we thus have to seek in older Eocene or earlier deposits, is theoretically required to have been a pentadactyle plantigrade animal provided with clavicles and possibly with bony epipubes. Such an animal, if it existed now, would probably be regarded as an Insectivore with more or less marked didelphous affinities.

In conclusion I desire to express my thanks to the President, to Dr. Günther, and to Dr. Rolleston for the ready access afforded me to the abundant materials for the study of the Canidæ in the Museum of the Royal College of Surgeons, the British Museum, and the Oxford Museum, to Sir Joseph Fayrer and to Mr. Wood-Mason, of the Indian Museum at Calcutta, for the great trouble they have been good enough to take in supplying me with specimens of Indian species, and to Professor Peters, of Berlin, for the loan of a skull of *V. corsac*.

[P.S.—I ought to mention that large additions have been made to this paper since it was read before the Society ; but I have deferred the consideration of the origin and relations of the domestic Dogs until the evidence which I am at present collecting is more complete. —July 4th, 1880.]

LIST OF WOODCUTS.

XXVI

ON THE APPLICATION OF THE LAWS OF EVOLUTION TO THE ARRANGEMENT OF THE VERTEBRATA AND MORE PARTICULARLY OF THE MAMMALIA.

Proceedings of the Scientific Meetings of the Zoological Society of London for the year 1880, *pp.* 649–662. (*Read December 14th,* 1880.)

THERE is evidence, the value of which has not been disputed, and which, in my judgment, amounts to proof, that, between the commencement of the Tertiary epoch and the present time, the group of the Equidæ has been represented by a series of forms, of which the oldest is that which departs least from the general type of structure of the higher Mammalia, while the latest is that which most widely differs from that type.

In fact, the earliest known equine animal possesses four complete subequal digits on the fore foot, three on the hind foot; the ulna is complete and distinct from the radius; the fibula is complete and distinct from the tibia; there are 44 teeth, the full number of canines being present, and the cheek-teeth having short crowns with simple patterns and early-formed roots. The latest, on the other hand, has only one complete digit on each foot, the others being represented by larger or smaller rudiments; the ulna is reduced and ankylosed with the radius; the fibula is still more reduced and partially ankylosed with the tibia; the canine teeth are partially or completely suppressed in the females; the first cheek-teeth usually remain undeveloped, and when they appear are very small; the other cheek-teeth have long crowns with highly complicated patterns and late-formed roots. The Equidæ of intermediate age exhibit intermediate characters.

With respect to the interpretation of these facts, two hypotheses, and only two, appear to be imaginable. The one assumes that these

successive forms of equine animals have come into existence independently of one another. The other assumes that they are the result of the gradual modification undergone by the successive members of a continuous line of ancestry.

As I am not aware that any zoologist maintains the first hypothesis, I do not feel called upon to discuss it. The adoption of the second, however, is equivalent to the acceptance of the doctrine of evolution, so far as Horses are concerned; and, in the absence of evidence to the contrary, I shall suppose that it is accepted.

Thus, since the commencement of the Eocene epoch, the animals which constitute the family of the Equidæ have undergone processes of modification of three kinds:—

1. There has been an excess of development of some parts in relation to others.

2. Certain parts have undergone complete or partial suppression.

3. Certain parts, which were originally distinct, have coalesced.

Employing the term "law" simply in the sense of a general statement of facts ascertained by observation, I shall speak of these three processes by which the *Eohippus* form has passed into *Equus* as the expression of a threefold law of evolution.

It is of profound interest to remark that this law, or generalized statement of the nature of the ancestral evolution of the Horses, is precisely the same as that which formulates the process of individual development in animals generally, from the period at which the broad characters of the group to which an animal belongs are discernible, onwards. After a mammalian embryo, for example, has taken on its general mammalian characters, its further progress towards its specific form is effected by the excessive growth of one part in relation to another, by the arrest of growth or the suppression of parts already formed, and by the coalescence of parts primarily distinct.

This coincidence of the laws of ancestral and individual development creates a strong confidence in the general validity of the former; and a belief that we may safely employ it in reasoning deductively from the known to the unknown. The astronomer who has determined three places of a new planet, calculates its place at any epoch however remote; and if the law of evolution is to be depended upon, the zoologist who knows a certain length of the course of that evolution in any given case, may with equal justice reason backwards to the earlier but unknown stages.

Applying this method to the case of the Horse, I do not see that

there is any reason to doubt that the Eocene *Equidæ* were preceded by Mesozoic forms which differed from *Eohippus* in the same way as *Eohippus* differs from *Equus*. And thus we are necessitated to conceive of a first term of the Equine series, which, if the law is of general validity, must needs have been provided with five subequal digits on each plantigrade foot, with complete, subequal antebrachial and crural bones, with clavicles, and with, at fewest, 44 teeth, the cheek-teeth having short crowns and simple-ridged or tuberculated patterns. Moreover, since Lartet's and Marsh's investigations have shown that the older forms of any given mammalian group have less developed cerebral hemispheres than the later, there is a *primâ facie* probability that this primordial Hippoid had a low form of brain. Further, since the existing Horse has a diffuse allantoic placentation, the primary form could not have presented a higher, and may have possessed a lower, condition of the various modes by which the fœtus derives nourishment from the parent among vertebrated animals.

Such an animal as this, however, would find no place in any of our systems of classification of the Mammalia. It would come nearest to the *Lemuroidea* and the *Insectivora*, though the non-prehensile pes would separate it from the former, and the placentation from the latter group.

A natural classification is one which associates together all those forms which are closely allied and separates them from the rest. But, whether in the ordinary sense of the word "alliance," or in its purely morphological sense, it is impossible to imagine groups of animals more closely allied than the primordial Hippoids are with their descendants. Yet, according to existing arrangements, the ancestors would have to be placed in one order of the class Mammalia and their descendants in another.

It may be suggested that it might be as well to wait until the primordial Hippoid is discovered before discussing the difficulties which will be created by its appearance. But the truth is, that the problem is already pressing in another shape. Numerous "Lemurs," with marked ungulate characters, are being discovered in the older Tertiaries of the United States and elsewhere; and no one can study the more ancient mammals with which we are already acquainted, without being constantly struck with the "Insectivorous" characters which they present. In fact, there is nothing in the dentition of either Primates, Carnivores, or Ungulates which is not foreshadowed in the Insectivora; and I am not aware that there is any means of deciding whether a given fossil skeleton, with skull, teeth, and limbs

almost complete, ought to be ranged with the Lemurs, the Insectivores, the Carnivores, or the Ungulates.

In whatever order of Mammals a sufficiently long series of forms has come to light, they illustrate the threefold law of evolution as clearly, though perhaps not so strikingly, as the Equine series does. Carnivores, Artiodactyles, and Perissodactyles all tend, as we trace them back through the Tertiary epoch, towards less modified forms which will fit into none of the recognized orders, but come closer to the Insectivora than to any other. It would, however, be most inconvenient and misleading to term these primordial forms "Insectivora," the mammals so called being themselves more or less specialized modifications of the same common type; and only, in a partial and limited sense, representatives of that type.

The root of the matter appears to me to be that the palæontological facts which have come to light in the course of the last ten or fifteen years have completely broken down existing taxonomical conceptions, and that attempts to construct fresh classifications upon the old model are necessarily futile.

The Cuvierian method, which most modern classifiers up to the time of the appearance of Haeckel's "Generelle Morphologie" have followed, has been of immense value in leading to the close investigation and the clear statement of the anatomical characters of animals. But its principle, the construction of sharp logical categories defined by such characters, was sapped when Von Baer showed that, in estimating the likenesses and unlikenesses of animals, development must be fully taken into account; and if the importance of individual development is admitted, that of ancestral development necessarily follows.

If the end of all zoological classification is the clear and concise expression of the morphological resemblances and differences of animals, then all such resemblances must have a taxonomic value. But they fall under three heads:—(1) those of adult individuals; (2) those of successive stages of embryological development or individual evolution; (3) those of successive stages of the evolution of the species, or ancestral evolution.

An arrangement is "natural" (that is, logically justifiable in view of the purpose of classification defined above) exactly in so far as it expresses the relations of likeness and unlikeness enumerated under these heads. Hence, in attempting to classify the Mammalia, we must take into account not only their adult and embryogenetic characters, but their morphological relations, in so far as the several groups represent different stages of evolution. And thus, just as

the persistent antagonism of Cuvier and his school to the essence of Lamarck's teachings (imperfect and objectionable as these often were in their accidents) turns out to have been a reactionary mistake, so Cuvier's no less definite repudiation of Bonnet's "échelle des êtres" must be regarded as another unfortunate effort to oppose the development of just biological conceptions. For though no one will pretend to defend Bonnet's "échelle" at the present day, the existence of a "scala animantium" is a necessary consequence of the doctrine of evolution; and its establishment constitutes, I believe, the foundation of scientific taxonomy.

If all the Mammalia are the results of a process of evolution analogous to that which has taken place in the case of the Equidæ, and if they exhibit different degrees of that process, then a natural classification will arrange them, in the first instance, according to the place which they occupy in the scale of evolution of the mammalian type, or the particular rung of the "scala mammalium" on which they stand. The determination of the position thus occupied by any group may, I think, be effected by the deductive application of the laws of evolution. That is to say, those groups which approach the non-mammalian Vertebrata most closely, present least inequality of development, least suppression and least coalescence of the fundamental parts of the type, must belong to earlier stages of evolution; while those which exhibit the contrary characters must appertain to later stages.

Judged from this point of view, there can be no doubt that the Monotremes embody that type of structure which constitutes the earliest stage of mammalian organization:—

1. The mammary glands are devoid of teats; and thus the essential feature of the mammal could hardly be presented under a simpler form.

2. There is a complete and deep cloaca, as in Vertebrata lower in the scale.

3. The openings of the ureters are *hypocystic*; that is to say, they open not into the bladder of these animals, but behind it, into the dorsal wall of the genito-urinary passage. As this answers to the neck of the allantois, the ureters of the Monotremes retain their primitive embryonic position.

4. There is no vagina apart from the genito-urinary passage; and the oviducts are not differentiated into distinct uterine and Fallopian regions.

5. The penis and the clitoris are attached to the ventral wall of the cloaca.

6. The epiphyses of the vertebræ are but slightly, or not at all, developed.[1]

7. The malleus is relatively very large; and the "processus gracilis," which is singularly long and strong, passes between the tympanic and the periotic bones to the pterygoid, with which it is firmly united. Thus the palato-pterygoid apparatus is directly connected by a "suspensorium" with the periotic, as in the Amphibia and Sauropsida. As in these, the representative of the incus is extremely small, and that of the stapes columelliform.

8. The coracoid is complete, distinct, and articulates with the sternum.

9. The hip-girdle is provided with large epipubes; and the iliac axis is inclined at a large angle to the sacral axis.

10. The corpus callosum is very small.

11. There appears to be no allantoic placenta, though, from the obvious remains of the ductus arteriosus and of the hypogastric arteries, there can be little doubt that the fœtus has a large respiratory allantois. It is quite possible that, with a large umbilical sac, there may be an imperfect "umbilical" placentation.

But, while the *Ornithorhynchus* and the *Echidna* are thus the representatives of the lowest stage of the evolution of the Mammalia, I conceive it to be equally unquestionable that, as Haeckel has already suggested, they are greatly modified forms of that stage—*Echidna*, on the whole, representing a greater, and *Ornithorhynchus* a less, departure from the general type. The absence of true teeth in both genera is an obvious sign of extreme modification. The long tongue, extraordinary external auditory passages, and relatively large convoluted brain of *Echidna*, and the cheek-pouches and horny mouthplates of *Ornithorhynchus*, are other indications of the same kind.

Hence the primary mammals, which were less modified, and the existence of which is necessarily postulated in the conception of the evolution of the group, cannot, without risk of confusion, be called Monotremata or Ornithodelphia, since in all probability they were as widely different from *Ornithorhynchus* and *Echidna* as the Insectivora are from the Edentata, or the Ungulata from *Rhytina*. Hence it will be convenient to have a distinct name, *Prototheria*,

[1] Dr. Albrecht ("Die Epiphysen und die Amphiomphalie der Säugethier-Wirbelkörper," Zoologischer Anzeiger, 1879, No. 18), while admitting that *Echidna* has no epiphyses, describes epiphyses of an incomplete character between the posterior twelve caudal vertebræ of *Ornithorhynchus*. So far as I am aware, the memoir, of which Dr. Albrecht has given a preliminary notice, has not yet been published; I content myself therefore with remarking hat my own recent observations are in harmony with Dr. Albrecht's statement.

for the group which includes these, at present, hypothetical embodiments of that lowest stage of the mammalian type, of which the existing Monotremes are the only known representatives.

A similar reasoning applies to the Marsupialia. In their essential and fundamental characters they occupy an intermediate position between the Prototheria and the higher mammals.

1. The mammary glands are provided with teats.

2. The cloaca is so greatly reduced that it is often said to have disappeared.

3. The openings of the ureters are *entocystic*; that is to say, the ureters open into what is called the "base" of the bladder, in front of the narrowed "neck" by which it passes into the tubular "urethra." This means, I conceive, that, morphologically, the bladder of the Marsupial represents the bladder of the Monotreme + the anterior part of the genito-urinary passage—the so-called "trigonum," if not more, of the bladder of the Marsupial, being the homologue of that anterior segment of the genito-urinary passage of the Monotreme.

4. There is a distinct and long vagina, quite separated from the cystic urethra, in the female; and the oviducts are differentiated into uterine and Fallopian portions.

5. The penis is large, and the corpora cavernosa are connected by fibrous tissue and muscles with the pelvis. The spongy body has a large bifurcated bulb; and Cowper's glands are very largely developed.

6. The vertebræ have distinct epiphyses.

7. The malleus is small; and its connections are similar to those which it possesses in the higher mammals. The incus is relatively larger, and the stapes more or less stirrup-shaped.

8. The coracoid is short, does not articulate with the sternum, and becomes ankylosed with the scapula.

9. The hip-girdle is provided with epipubes, usually of large size and well ossified; and the iliac axis is inclined at a small angle to the sacral axis.

10. The corpus callosum is small.

11. In the few forms of which the fœtus is known there is no allantoic placenta; while the umbilical sac is so large that the possibility of the existence of a transitory umbilical placentation must be taken into account.

It will be observed that in the characters 1, 2, 3, 4, 5, 6, 7, 8, and the latter part of the 9th, the Marsupials agree with the higher mammals; while in the former part of the 9th, the 10th, and the

11th they present Prototherian characters. So far, therefore, they constitute an intermediate type between that of the Prototheria and that of the higher mammals, which may be termed that of the *Metatheria*. And if there were any known animals which combined these characters, with a complete double dentition, unmodified pentadactyle manus and pes, and normal uterogestation, they would furnish us with the exact transition between the Prototheria and the higher mammals, which must have existed if the law of evolution is trustworthy.

No known Marsupial, however, possesses these additional characters. None has more than a single successional tooth on each side of each jaw; and, as Prof. Flower (to whom we owe the highly important demonstration of this fact) has pointed out, the question arises whether we have here a primary dentition with only one secondary tooth, or a secondary dentition with only one tooth of the primary set left. I have no doubt that the answer given to this question by Prof. Flower is correct, and that it is the milk-dentition of which only a vestige is left in the Marsupialia. Among existing Rodents, in fact, all conditions of the milk-dentition exist, from a number equal to that of the permanent incisors and premolars (as in the Rabbit[1]) to none at all.

The same thing is observed in the Insectivora, where the Hedgehog, and probably *Centetes*, have a full set of milk-teeth, while none have yet been found in the Shrews. In these cases it is obvious that the milk-dentition has gradually been suppressed in the more modified forms; and I think that there can be no reasonable doubt that the existing Marsupials have undergone a like suppression of the deciduous teeth, in the course of their derivation from ancestors which possessed a full set.

Again, no existing Marsupial possesses an unmodified pentadactyle pes. If the hallux is present, it presents an extensive movement in adduction and abduction; in fact, the pes is prehensile. This is the case in the *Phascolomyidæ*, *Phalangistidæ*, *Phascolarctidæ*, and *Didelphidæ*. The *Dasyuridæ* present the same type of pes, with the hallux reduced or suppressed. Hence, considering the relations of the *Macropodidæ* and the *Peramelidæ* with the Phalangers, it seems

[1] The deciduous molars and the posterior deciduous upper incisors of the Rabbit have long been known. But I have recently found that unborn Rabbits possess, in addition, two anterior upper and two lower deciduous incisors. Both are simple conical teeth, the sacs of which are merely embedded in the gum. The upper is not more than one-hundredth of an inch long, the lower rather larger. It would be interesting to examine fœtal Guinea-pigs in relation to this point: at present they are known to possess only the hindmost deciduous molars, and, so far, agree with the Marsupials.

likely that the hind foot in these groups is also a reduced prehensile pes; in which case this special modification of the foot would characterize the whole of the existing *Marsupialia.*

Thirdly, the most marked peculiarities of the reproductive organs and processes in the Marsupial are in no wise transitional, but are singularly specialized characters. The suspension of the scrotum in front of the root of the penis is unlike any arrangement in the higher mammals; and the development of the bulb and of Cowper's glands is in excess of anything observable in them. In the female, the cystic urethra is as completely separated from the vagina as it is in the higher mammals; while the doubling of the vagina must, in my opinion, also be considered a special peculiarity which leads from, rather than towards, the higher mammals. In a Monotreme, in fact, the anterior end of the genito-urinary passage exhibits two very short dilatations or cornua, one on each side. In the middle line, a little distance behind these, the ureters open on a prominent ridge-like papilla. The opening of the bladder lies in front of and below the genital cornua. Now, if we compare this arrangement with that which obtains in the lower forms of the higher Mammalia, we find that the ureteric papillæ have separated laterally and moved forwards, in such a manner as to occupy the base of the bladder, and the genital cornua come to lie behind and somewhat dorsad of them. At the same time a longitudinal separation has taken place between what may be called the "ureteric" region of the genito-urinary passage and the "genital" region. The first is taken into the bladder and becomes connected by a longer or shorter "cystic urethra" with the latter, which is converted into the longer or shorter vagina. In the Marsupial the same general modification has taken place; but the "genital cornua" become immensely elongated, and give rise to the so-called "double" vagina.

Lastly, the marsupium, where it exists, is a no less special feature of the Marsupialia, and, like the peculiarities of the female genital organs, appears to be related with the abnormally early birth of the fœtus. Among the higher Mammalia, it is well known that the fœtus is born in a relatively much earlier state in some cases than in others, even among closely allied species. Thus Rabbits are born hairless and blind, while Hares are born hairy and with their eyes open. I think it probable, from the character of the pes, that the primitive forms whence the existing Marsupialia have been derived, were arboreal animals; and it is not difficult, I conceive, to see that, with such habits, it may have been highly advantageous to an animal to get rid of its young from the interior of its body at as early a period of

development as possible, and to supply it with nourishment during the later periods through the lacteal glands, rather than through an imperfect form of placenta.

However this may be, the characters of the existing Marsupialia leave no doubt on my mind that they are greatly modified members of the Metatherial type; and I suspect that most, if not all, of the Australian forms are of comparatively late origin. I think it probable that the great majority of the Metatheria, of which I doubt not a great multitude will shortly be discovered in Mesozoic formations, differed widely from our existing Marsupials—not only lacking the pouch, as do some existing "Marsupialia," but possessing undivided vaginæ, and probably bringing forth their young not earlier than existing Carnivores and Rodents do, the nutrition of the fœtus during prolonged gestation being provided for, in all probability, by an umbilical placental apparatus, and its respiration by a non-placental allantois.

In the remaining group of the Mammalia, hitherto spoken of as the "higher Mammalia,"—

1. The mammary glands are provided with teats.[1]

2. The cloaca has usually disappeared. Sometimes, however (Beavers, Sloths), a shallow cloaca is present, especially in the female.

3. The openings of the ureters are always entocystic; but their position varies greatly, from close to the neck (e.g. *Sorex*) to the anterior end of the bladder (e.g. *Hyrax*).

4. There is a distinct vagina, which is almost always undivided. The oviducts are differentiated into uterine and Fallopian portions.

5. The penis is usually large, the bulb single or partially divided, and the corpora cavernosa almost always directly attached to the ischia.

6. The vertebræ have epiphyses.

7. The malleus is usually small, the incus relatively large, the stapes stirrup-shaped.

8. The coracoid is almost always much reduced, and it is ankylosed with the scapula.

9. The iliac axis makes a small angle with the sacral axis; and there is no epipubis, or only a fibrous vestige of it.

10. The corpus callosum and the anterior commissure vary widely. In such forms as *Erinaceus* and *Dasypus* they are almost Monotreme-like.

[1] The only exception known to me is the Cape Mole (*Chrysochloris*), which, according to Peters, has none.

11. The fœtus is connected with the uterus of the mother by an allantoic placenta. The umbilical sac varies in size; and in some lower forms (e.g. *Lepus*) it is, at first, highly vascular, and perhaps plays a quasi-placental part during the early stages of development.

It is obvious that, in all these respects, we have the mammalian type in a higher stage of evolution than that presented by the Prototheria and the Metatheria. Hence we may term forms which have reached this stage the *Eutheria.*

It is a fact, curiously in accordance with what might be expected on evolutionary principles, that while the existing members of the Prototheria and the Metatheria are all extremely modified, there are certain forms of living Eutheria which depart but little from the general type. For example, if *Gymnura* possessed a diffuse placentation, it would be an excellent representative of an undifferentiated Eutherian. Many years ago, in my lectures at the Royal College of Surgeons, I particularly insisted on the central position of the Insectivora among the higher Mammalia; and further study of this order and of the Rodentia has only strengthened my conviction, that any one who is acquainted with the range of variation of structure in these groups possesses the key to every peculiarity which is met with in the Primates, the Carnivora, and the Ungulata. Given the common plan of the Insectivora and of the Rodentia, and granting that the modifications of the structure of the limbs, of the brain, and of the alimentary and reproductive viscera which occur among them may exist and accumulate elsewhere, and the derivation of all the *Eutheria* from animals which, except for their simpler placentation, would be Insectivores, is a simple deduction from the law of evolution.

There is no known Monotreme which is not vastly more different from the Prototherian type, and no Marsupial which has not far more widely departed from the Metatherian type, than *Gymnura*, or, indeed, *Erinaceus*, have from the Eutherian type.

The broadest physiological distinction between the Prototheria, the Metatheria, and the Eutheria, respectively, lies in the differences which the arrangements for prolonging the period of intra-uterine and extra-uterine nutrition by the parent present in each. The possibility of a higher differentiation of the species is apparently closely connected with the length of this period. Similarly, the broadest morphological distinction which can be drawn among the *Eutheria* lies in their placentation. All forms of deciduate placentation commence by being non-deciduate; and the intimate connection

of the fœtal with the maternal structures is subsequent to their loose union. Hence *Eutheria*, with deciduate placentæ, are in a higher stage of evolution than those with non-deciduate placentæ.

In discussing the relations of the various existing groups of the higher Mammalia with one another, it would be a mistake to attempt to trace any direct genetic connection between them. Each, as the case of the Equidæ suggests, has probably had a peculiar line of ancestry; and, in these lines, Eutherian forms with deciduate placentation constitute the latest term, Eutherian forms with non-deciduate placentation the next latest, Metatherian forms the next, Prototherian forms the earliest among those animals which, according to existing definition, would be regarded as Mammals.

The accompanying Table (p. 469) presents, at a glance, the arrangement of the Mammalia in accordance with the views which I have endeavoured to express. The sign O marks the places on the scheme which are occupied by known Mammals; while × indicates the groups of which nothing is known, but the former existence of which is deducible from the law of evolution.

I venture to express a confident expectation that investigation into the Mammalian fauna of the Mesozoic epoch will sooner or later fill up these blanks. But if deduction from the law of evolution is to be justified thus far, it may be trusted much further. If we may confidently expect that *Eohippus* had a pentadactyle claviculate ancestor, then we may expect, with no less confidence, that the *Prototheria* proceeded from ancestors which were not mammals—in so far as they had no mammary glands, and in so far as the mandible was articulated with a quadrate bone, of which the malleus of the true mammal is the reduced representative. Probably also the corpus callosum had not appeared as a distinct structure.

Our existing classifications have no place for this "submammalian" stage of evolution (already indicated by Haeckel under the name of *Promammale*). It would be separated from the Sauropsida by its two condyles, and by the retention of the left as the principal aortic arch; while it would probably be no less differentiated from the Amphibia by the presence of an amnion and the absence of branchiæ at any period of life. I propose to term the representatives of this stage *Hypotheria*; and I do not doubt that when we have a fuller knowledge of the terrestrial Vertebrata of the later Palæozoic epochs, forms belonging to this stage will be found among them Now, if we take away from the Hypotheria the amnion and the corpus callosum, and add the functional branchiæ—the existence of which in the ancestors of the Mammalia is as clearly indicated by

Stages of Evolution.	Mammalia.		Primates.	Marsupialia.	Lemuroidea.	Rodentia.	Proboscidea.	Sirenia.	Ungulata.	Hydracoidea.	Insectivora.	Cetacea.	Carnivora.	Cheiroptera.	Edentata.	Monotremata.
Eutheria .	1. Teats. 2. Allantoic placenta. 3. Euroteric apertures entocystic. 4. Small malleus. 5. Reduced coracoid. 6. Epipubis rudimentary or absent. 7. Two occipital condyles and an osseous basioccipital. 8. Amnion present. 9. A corpus callosum. 10. No branchiæ.	Placenta. deciduate.	O			O	O			O	O		O	O	O (*Orycteropa*. *Myrmecophaga*.)	
		non-deciduate.	×		O			O	O			O			O (*Manis*.)	
Metatheria	1, 3, 4, 5, 7, 8, 9, 10 as above. ii. and vi. as below.	. . . .	×	O	×	×	×	×	×	×	×	×	×	×	×	
Prototheria	7, 8, 9, 10 as above. i. No teats. ii. No allantoic placenta. iii. Ureteric apertures hypocystic. iv. Large malleus. v. Complete coracoid. vi. Large epipubes.	. . . .	×	×	×	×	×	×	×	×	×	×	×	×	×	O
Hypotheria	7, 8, i., ii., iii., iv., v., vi., as above. *a*. No mammary gland. *b*. Mandible articulating with quadrate. *c*. No corpus callosum.	. . . .	×	×	×	×	×	×	×	×	×	×	×	×	×	×

their visceral arches and clefts, as the existence of complete clavicles in the ancestral Canidæ is indicated by their vestiges in the dog—the Hypotheria, thus reduced, at once take their place among the Amphibia. For the presence of branchiæ implies that of an incompletely divided ventricle and of numerous aortic arches, such as exist in the mammalian embryo, but are more or less completely suppressed in the course of its development.

Thus I regard the Amphibian type as the representative of the next lower stage of vertebrate evolution ; and it is extremely interesting to observe that even the existing Amphibia present us with almost every degree of modification of the type, from such forms as the oviparous, branchiate, small-lunged *Siredon* and *Menobranchus*, which stand in the same relation to it as *Gymnura* to the Eutheria, to the exclusively air-breathing Salamanders and Frogs, in which the period of intraovular development, either within the uterus itself or in special receptacles, may be as much prolonged as it is in the Mammalia.

A careful study, on full materials, of the development of the young of such forms as *Hylodes* will probably throw great light on the nature of the changes which ended in the suppression of the branchiæ, and the development of the amnion and of the extra-abdominal part of the allantois in the fœtus of the higher Vertebrata.

The recent researches of Boas [1] on the structure of the heart and the origin of the pulmonary arteries of *Ceratodus* fell into my hands when I happened to be working afresh at the subject, and had arrived, so far as the heart is concerned, at results which are entirely confirmatory of his. This wonderful creature seems contrived for the illustration of the doctrine of Evolution. Equally good arguments might be adduced for the assertion that it is an amphibian or a fish, or both, or neither—the reason of this being that, as it appears to me, *Ceratodus* is an extraordinarily little-modified representative of that particular stage of vertebrate evolution of which both the typical Fishes and the typical Amphibia are special modifications. I think it will be convenient to have a name for the representatives of this stage ; and I propose that of *Herpetichthyes*.

If we were to take away from *Ceratodus* the membrane-bones of the head and the pneumatocœle, and slightly simplify the structure of the heart, the result would be an animal which would undoubtedly be classed among the *Chimeroidei* ; and if, in such a Chimæroid, the

[1] "Ueber Herz und Arterienbogen bei *Ceratodus* und *Protopterus*," Morph. Jahrbuch, 1880.

lamellar septa of the branchiæ were not reduced, as they are in the Chimæroids, while the opercular fold remained undeveloped, the product would be a little-modified representative of the Selachian group, to which, among actually known forms, *Heptanchus* and *Cestracion* present the nearest approximations. Vertebrated animals in this stage of evolution may be termed *Chondrichthyes.*

Suppose the limbs and the genital ducts of the Chondrichthyan stage to be undeveloped, and let the two nasal sacs be represented by a partially divided sac with a single external aperture, the result will be a still lower grade of vertebrate life, which may be termed *Myzichthyes*, represented only by the greatly modified Lampreys and Hags of the existing fauna.

Finally, let the head retain its primitive segmentation, and the heart its primitive character of a contractile tube, and we reach, in the *Hypichthyes*, a stage of simplification of the vertebrate type, from which it would be difficult to remove any essential feature without reaching a point at which it is questionable whether an animal should be called "vertebrate." This stage is at present represented only by a singularly modified form, the living *Amphioxus.*

Thus, in the order of Evolution all the Vertebrata hitherto considered may be arranged in nine stages :-- 1, that of the *Hypichthyes* ; 2, that of the *Myzichthyes* ; 3, that of the *Chondrichthyes*; 4, that of the *Herpetichthyes*; 5, that of the *Amphibia*; 6, that of the *Hypotheria* ; 7, that of the *Prototheria* ; 8, that of the *Metatheria*; and, 9, that of the *Eutheria.* All these stages, except that of the *Hypotheria*, are represented by existing groups of vertebrated animals, which in most cases are composed of greatly modified forms of the type to which they belong, only the Amphibia and the Eutheria exhibiting near approximations to the unmodified type in some of their existing members.

It will be observed that I have omitted to mention the Ganoid and the Teleostean Fishes and the Sauropsida. I have done so because they appear to me to lie off the main line of evolution—to represent, as it were, side tracks starting from certain points of that line. The Ganoidei and the Teleostei I conceive to stand in this relation to the stage of the Herpetichthyes, and the Sauropsida to the stage of the Amphibia.

There is nothing, so far as I can see, in the organization of the Ganoid and Teleostean fishes which is not readily explicable by the application of the law of Evolution to the Herpetichthyes. They may

be interpreted as effects of the excessive development, reduction, or coalescence of the parts of a Herpetichthyan.[1]

Similarly, the suppression of the branchiæ, the development of an amnion, and of a respiratory extra-abdominal allantois, and that enlargement of the basioccipital relatively to the exoccipitals which gives rise to a single skull-condyle, is all the change required to convert a Urodele Amphibian into a Lizard. It is needless to recapitulate the evidence of the transition from the Reptilian to the Bird type which the study of extinct animal remains has brought to light.

The scheme of arrangement of the Vertebrata which naturally flows from the considerations now brought forward will stand thus :—

Stages of Evolution.	Representative Groups.			
9. *Eutheria*	*Monodelphia.*			
	O			
8. *Metatheria*	*Marsupialia.*			
	O			
7. *Prototheria*	*Monotremata.*			
	O			
6. *Hypotheria*	×	*Sauropsida*	*Aves.* *Reptilia.*	
		O		
5. *Amphibia*	*Amphibia*	×		
	O			
4. *Herpetichthyes*	*Dipnoi*	×	*Osteichthyes*	*Ganoidei.* *Teleostei.*
	O		O	
3. *Chondrichthyes*	*Chimæroidei*	×	×	
	O			
	Selachii.	×	×	
	O			
2. *Myzichthyes*	*Marsipobranchii*	×	×	
	O			
1. *Hypichthyes*	*Pharyngobranchii*	×	×	
	O			

It appears to me that everything which is at present known respecting the Vertebrata of past epochs agrees with the assumption that the law which expresses the process of ancestral evolution of the higher Mammalia is of general application to all the Vertebrata. If this is admitted, I think it necessarily follows that the Vertebrata must have passed successively through the stages here indicated, and that the progress of discovery, while it will obliterate the lines of demarcation between these stages, and convert them into a continuous series of small differentiations, will yield no vertebrate form for which a place does not exist in the general scheme.

[1] That the heart of *Butirinus* affords a complete transition between the characteristically Ganoid and the characteristically Teleostean heart, has recently been proved by Boas (Morphol. Jahrbuch). Thus the last remnant of the supposed hiatus between the Ganoids and the Teleosteans vanishes.

XXVII

THE HERRING.

Nature, vol. xxiii., 1881, *pp.* 607–613. (*A Lecture delivered at the National Fishery Exhibition, Norwich, April 21st*, 1881.)

IT is now nineteen years since my attention was first specially directed to the natural history of the herring, and to the many important economical and legal questions connected with the herring fisheries. As a member of two successive Royal Commissions, it fell to my lot to take part in inquiries held at every important fishing station in the United Kingdom between the years 1862 and 1865, and to hear all that practical fishermen had to tell about the matter; while I had free access to the official records of the Fishery Boards. Nor did I neglect such opportunities as presented themselves of studying the fish itself, and of determining the scientific value of the terms by which, in the language of fishermen, the various conditions of the herring are distinguished.

Diligent sifting of the body of evidence thus collected and passed under review, led to the satisfactory clearing away in my own mind of some of the obscurities which, at that time, surrounded the natural history of the fish. But many problems remained, the solution of which was not practicable by investigations which, after all, were only incidents in the course of a large inquiry, embracing a vast number of topics beside herrings and herring fisheries; and it is only within the last few years that the labours of the German West Baltic Fishery Commission have made such large additions to the state of our knowledge in 1865, that the history of the herring is brought within measurable distance of completeness.

Considering the vast importance of the herring fisheries of the Eastern Counties, it occurred to me when the President of the National Fishery Exhibition did me the honour to ask me to address

you, that nothing could be more likely to interest my audience than a summary statement of what is now really known about a fish which, from a fisherman's point of view, is probably the chief of fishes.

I am aware that I may lay myself open to the application of the proverb about carrying coals to Newcastle, if I commence my observations with a description of the most important distinctive characters of a fish which is so familiar to the majority of my hearers. And perhaps it is as well that I should at once express my belief that most of you are as little likely to mistake a herring for anything else as I am. Nay, I will go further. I have reason to believe that any herring-merchant, in a large way of business, who may be here, knows these fish so much better than I do, that he is able to discriminate a Yarmouth herring from a Scotch herring, and both from a Norway herring ; a feat which I could not undertake to perform. But then it is possible that I may know some things that he does not. He is very unlike other fishermen and fish-merchants with whom I have met, if he has any but the vaguest notions of the way of life of the fish ; or if he has heard anything about those singularities of its organisation which perplex biologists ; or if he can say exactly how and why he knows that a herring is not a sprat, a shad, or a pilchard. And all kinds of real knowledge and insight into the facts of nature do so bear upon one another and turn out in strange ways practically helpful, that I propose to pour out my scientific budget, in the hope that something more may come of it than the gratification of intelligent curiosity.

If any one wants to exemplify the meaning of the word "fish" he cannot choose a better animal than a herring. The body, tapering to each end, is covered with thin, flexible scales, which are very easily rubbed off. The taper head, with its underhung jaw, is smooth and scaleless on the top ; the large eye is partly covered by two folds of transparent skin, like eyelids—only immovable and with the slit between them vertical instead of horizontal ; the cleft behind the gill cover is very wide, and, when the cover is raised, the large red gills which lie beneath it are freely exposed. The rounded back bears the single moderately long dorsal fin about its middle. The tail fin is deeply cleft, and on careful inspection small scales are seen to be continued from the body, on to both its upper and its lower lobes, but there is no longitudinal scaly fold on either of these. The belly comes to an edge, covered by a series of sharply keeled bony shields between the throat and the vent ; and behind the last is the anal fin, which is of the same length as the dorsal fin. There is a pair of fore-limbs, or pectoral fins, just behind the head ; and a pair of hind-

limbs, or ventral fins, are situated beneath the dorsal fin, a little behind a vertical line drawn from its front edge, and a long way in front of the vent. These fins have bony supports or rays, all of which are soft and jointed.

Like most fishes, the herring is propelled chiefly by the sculling action of the tail-fin, the rest serving chiefly to preserve the balance of the body, and to keep it from turning over, as it would do if left to itself, the back being the heaviest part of the fish.

The mouth of the herring is not very large, the gape extending back only to beneath the middle of the eye, and the teeth on the upper and lower jaws are so small as to be hardly visible. Moreover, when a live herring opens its mouth, or when the lower jaw of a dead herring is depressed artificially, the upper jaw, instead of remaining fixed and stationary, travels downwards and forwards in such a manner as to guard the sides of the gape. This movement is the result of a curious mechanical arrangement by which the lower jaw pulls upon the upper, and I suspect that it is useful in guarding the sides of the gape when the fish gulps the small living prey upon which it feeds.

The only conspicuous teeth, and they are very small, are disposed in an elongated patch upon the tongue, and in another such patch, opposite to these, on the fore part of the roof of the mouth. The latter are attached to a bone called the vomer, and are hence termed vomerine teeth. But, if the mouth of a herring is opened widely, there will be seen, on each side, a great number of fine, long, bristle-like processes, the pointed ends of which project forwards. These are what are termed the gill-rakers, inasmuch as they are fixed, like the teeth of a rake, to the inner sides of those arches of bone on the outer sides of which the gills are fixed. The sides of the throat of a herring, in fact, are as it were cut by four deep and wide clefts which are separated by these gill arches, and the water which the fish constantly gulps in by the mouth flows through these clefts, over the gills and out beneath the gill covers, aërating the blood, and thus effecting respiration, as it goes. But since it would be highly inconvenient, and indeed injurious, were the food to slip out in the same way, these gill rakers play the part of a fine sieve, which lets the water strain off, while it keeps the food in. The gill rakers of the front arches are much longer than those of the hinder arches, and as each is stiffened by a thread of bone developed in its interior, while, at the same time, its sides are beset with fine sharp teeth, like thorns on a brier, I suspect that they play some part in crushing the life out of the small animals on which the herrings prey.

Between these arches there is, in the middle line, an opening which leads into the gullet. This passes back into a curious conical sac which is commonly termed the stomach, but which has more the character of a crop. Coming off from the under side of the sac and communicating with it by a narrow opening, there is an elongated tubular organ, the walls of which are so thick and muscular that it might almost be compared to a gizzard. It is directed forwards, and opens by a narrow prominent aperture into the intestine, which runs straight back to the vent. Attached to the commencement of the intestine, there is a score or more of larger and shorter tubular organs which are called the pyloric cæca. These open into the intestine, and their apertures may be seen on one side of it, occupying an oval space, in the middle of which they are arranged three in a row.

The chief food of the herring consists of minute Crustacea, some of them allied to the shrimps and prawns, but the majority belonging to the same division as the common *Cyclops* of our fresh waters. These tenant many parts of the ocean in such prodigious masses that the water is discoloured by them for miles together, and every sweep of a fine net brings up its tens of thousands.

Everybody must have noticed the silvery air-bladder of the herring, which lies immediately under the backbone, and stretches from close to the head to very near the vent, being wide in the middle and tapering off to each end. In its natural state, it is distended with air; and, if it is pricked, the elastic wall shrinks and drives the air out, as if it were an indiarubber ball. When the connections of this air-bladder are fully explored it turns out to be one of the most curious parts of the organisation of the whole animal.

In the first place, the pointed end of the sac or crop into which the gullet is continued runs back into a very slender duct which turns upwards and eventually opens into the middle of the air-bladder. The canal of this duct is so very small and irregularly twisted, that, even if the air-bladder is squeezed, the air does not escape into the sac. But, if air is forced into the sac by means of a blow-pipe, the air passes without much difficulty the other way, and the air-bladder becomes fully distended. When the pressure is removed, however, the air-bladder diminishes in size to a certain extent, showing that the air escapes somewhere. And if the blowing up of the air-bladder is performed while the fish is under water, a fine stream of air-bubbles may be seen to escape close to the vent. Careful anatomical investigation, in fact, shows that the air-bladder does not really end at the point where its silvery coat finishes, but that a delicate tube is

continued thence to the left side of the vent, and there ends by an opening of its own.

Now the air-bladder of all fishes is, to begin with, an outgrowth from the front part of the alimentary canal, and there are a great many fishes in which, as in the herring, it remains throughout life in permanent communication with the gullet. But it is rare to find the duct so far back as in the herring; and, at present, I am not aware that the air-bladder opens externally in any fishes except the herring and a few of its allies.

There is a general agreement among fishermen that herrings sometimes make a squeaking noise when they are freshly taken out of the water. I have never heard this sound myself, but there is so much concurrent testimony to the fact that I do not doubt it; and it occurs to me that it may be produced when the herrings are quickly brought up from some depth by means of this arrangement. For under these circumstances the air, which the air-bladder contains, expands to such a degree, on being relieved from the pressure of the water, that deep-sea fishes with a closed air-bladder which are brought to the surface rapidly are sometimes fairly turned inside out by the immense distension, or even bursting, of the air-bladder. If the same thing should happen to the herring the like misfortune would not befall it, for the air would be forced out of the opening in question, and might readily enough produce the squeak which is reported. The common Loach[1] is said to produce a piping sound by expelling the air which this fish takes into its intestine for respiratory purposes.

At the opposite end of the air-bladder there is an even more curious arrangement. The silvery coat of the air-bladder ends in front just behind the head. But the air-bladder itself does not terminate here. Two very fine canals, each of which is not more than a two hundredth of an inch in diameter, though it is surrounded by a relatively thick wall of cartilage, pass forward, one on each side, from the air-bladder to the back of the skull. The canals enter the walls of the skull, and then each divides into two branches. Finally, each of these two dilates into a bag which lies in a spheroidal chamber of corresponding size and form; and, in consequence of the air which they contain, these bags may be seen readily enough shining through the side walls of the skull, the bone of which has a peculiar structure where it surrounds them. Now these two bags, which constitute the termination of the air-bladder on each side, are

[1] See Müller, "Ueber Fische welche Töne von sich geben," *Archiv für Physiologie*, 1857, p. 267. The herring is not mentioned in Müller's list of vocal fishes.

in close relation with the organ of hearing. Indeed, a process of that organ projects into the front chamber on each side, and is separated by only a very delicate partition from the terminal sac of the air-bladder. Any vibrations of the air in these sacs, or any change in the pressure of the air in them, must thus tell upon the hearing apparatus.

There is no doubt about the existence of these structures which, together with the posterior opening of the air-bladder, were most accurately described, more than sixty years ago, by the eminent anatomist Weber, but I am afraid we are not much wiser regarding their meaning than we were when they were first made known. In fishes in general there can be little doubt that the chief use of the air-bladder is to diminish the specific gravity of the fish and, by rendering its body of nearly the same weight as so much water, to render the business of swimming easier. In those fishes in which the passage of communication between the air-bladder and the alimentary canal is closed, the air is no doubt secreted into the air-bladder by its vessels, which are often very abundant. In the herring, the vessels of the air-bladder are very scanty: and it seems probable that the air is swallowed and forced into the air-bladder just as the loach swallows air and drives it into its intestine. And, as I have already suggested, it may be that the narrow posterior canal which leads from the air-bladder to the exterior is a sort of safety-valve allowing the air to escape, when the fish, rapidly ascending or descending, alters the pressure of the water upon the contained air.

This hypothesis may be put forward with some show of probability, but I really find it difficult to suggest anything with respect to the physiological meaning of the connection between the air-bladder and the ear. Nevertheless such an elaborate apparatus must have some physiological importance; and this conclusion is strengthened by the well-known fact that there are a great many fishes in which the air-bladder and the ear become connected in one way or another. In the carp tribe, for example, the front end of the air-bladder is connected by a series of little bones with the organ of hearing, which is, as it were, prolonged backwards to meet these bones in the hinder end of the skull. But here, the air-bladder, which is very large, may act as a resonator; while, in the herring, the extreme narrowness of the passages which connect the air-bladder with the ear renders it difficult to suppose that the organ can have any such function.

In addition to the singular connection of the ear with the exterior by the roundabout way of the air-bladder, there are membranous

spaces in the walls of the skull by which vibrations can more directly reach the herring's ear. And there is no doubt that the fish is very sensitive to such vibrations. In a dark night, when the water is phosphorescent or, as the fishermen say, there is plenty of "merefire," it is a curious spectacle to watch the effect of sharply tapping the side of the boat as it passes over a shoal. The herrings scatter in all directions, leaving streaks of light behind them, like shooting stars.

The herring, like other fishes, breathes by means of the gills—the essential part of which consists of the delicate, highly-vascular filaments, which are set in a double row on the outer faces of each of the gill arches. The venous blood which returns from all parts of the body to be collected in the heart, is pumped thence into the gills, and there exchanges its excess of carbonic acid gas for the gaseous oxygen which is dissolved in sea-water. The freedom of passage of the water, and the great size and delicacy of the gills, facilitate respiration when the fish is in its native element; but the same peculiarities permitting of the rapid drying and coherence of the gills, and thus bringing on speedy suffocation, render its tenure of life, after removal from the water, as short as that of any fish. It may be observed, in passing, that the wide clefts behind the gill-covers of the herring have some practical importance, as the fish, thrusting its head through the meshes of the drift-net, is caught behind them and cannot extricate itself. In the herring, the upper end of the last gill cleft is not developed into a sac or pouch, such as we shall find in some of its near neighbours.

The only other organs of the herring, which need be mentioned at present, are the milt and roe, found in the male and female herring respectively.

These are elongated organs attached beneath the air-bladder, which lie, one on each side of the abdominal cavity, and open behind the vent by an aperture common to the two. The spermatic fluid of the male is developed in the milt and the eggs of the female in the roe. These eggs, when fully formed, measure from one-sixteenth to one-twenty-fifth of an inch in diameter; and, as, in the ripe female the two roes or ovaries stretch from one end of the abdominal cavity to the other, occupying all the space left by the other organs, and distending the cavity, the number of eggs which they contain must be very great. Probably 10,000 is an under-estimate of the number of ripe eggs shed in spawning by a moderate-sized female herring. But I think it is safer than the 30,000 of some estimates, which appear to me to be made in forgetfulness of the very simple anatomical

considerations that the roe consists of an extensive vascular framework as well as of eggs; and, moreover, that a vast number of the eggs which it contains remain immature, and are not shed at the time of spawning.

In this brief account of the structure of the herring I have touched only on those points which are peculiarly interesting, or which bear upon what I shall have to say by and by. An exhaustive study of the fish from this point of view alone would require a whole course of lectures to itself.

The herring is a member of a very large group of fishes spread over all parts of the world, and termed that of the *Clupeidæ*, after *Clupea*, the generic name of the herring itself. Our herring, the *Clupea harengus*, inhabits the White Sea and perhaps some parts of the Arctic Ocean, the temperate and colder parts of the Atlantic, the North Sea, and the Baltic, and there is a very similar, if not identical, species in the North Pacific. But it is not known to occur in the seas of southern Europe, nor in any part of the intertropical ocean, nor in the southern hemisphere.

There are four British fishes which so closely resemble herrings, externally and internally, that, though practical men may not be in any danger of confounding them, scientific zoologists have not always succeeded in defining their differences. These are the Sprat, the Allice and Twaite Shads, and the Pilchard.

The sprat comes nearest; indeed young herrings and sprats have often been confounded together, and doubts have been thrown on the specific distinctness of the two. Yet if a sprat and a young herring of the same size are placed side by side, even their external differences leave no doubt of their distinctness. The sprat's lower jaw is shorter; the shields in the middle of the belly have a sharper keel, whence the ventral edge is more like a saw; and the ventral fin lies vertically under the front edge of the dorsal fin, or even in front of it; while in the herring, though the position of the ventral fin varies a little, it lies more or less behind the front margin of the dorsal fin. The anal fin is of the same length as the dorsal, in the herring, longer than the dorsal in the sprat. But the best marks of distinction are the absence of vomerine teeth in the sprat, and the smaller number of pyloric cæca, which do not exceed nine, their openings being disposed in a single longitudinal series.

Shads and pilchards have a common character by which they are very easily distinguished from both sprat and herring. There is a horizontal fold of scaly skin on each side of the tail above and below the middle line. Moreover they have no teeth in the inside of the

mouth, and their pyloric cæca are very numerous—a hundred or more—their openings being disposed five or six in a row.

The shads have a deep narrow notch in the middle line of the upper jaw, which is absent in the pilchard. The intestine of the shad is short and straight, like that of the herring; while that of the pilchard is long and folded several times upon itself.

Both of these fishes, again, possess a very curious structure, termed an accessory branchial organ, which is found more highly developed in other fishes of the herring family, and attains its greatest development in a fresh-water fish, the *Heterotis*, which inhabits the Nile. This organ is very rudimentary in the shad (in which it was discovered by Gegenbaur[1]), but it is much larger in the pilchard, in which, so far as I know, it has not heretofore been noticed. In *Chanos* and several other Clupeoid fishes it becomes coiled upon itself, and in *Heterotis* the coiled organ makes many turns. The organ is commonly supposed to be respiratory in function; but this is very doubtful.

Herrings which have attained maturity and are distended by the greatly enlarged milt or roe are ready to shed the contents of these organs or, as it is said, to spawn. In 1862, we found a great diversity of opinion prevailed as to the time at which this operation takes place, and we took a great deal of trouble to settle the question, with the result which is thus stated in our Report:—

"We have obtained a very large body of valuable evidence on this subject, derived partly from the examination of fishermen and of others conversant with the herring fishery; partly from the inspection of the accurate records kept by the fishery officers at different stations, and partly from other sources; and our clear conclusion from all this evidence is, that the herring spawns at two seasons of the year, in the spring and in the autumn. We have hitherto met with no case of full or spawning herrings being found, in any locality, during what may be termed the solstitial months, namely June and December; and it would appear that such herrings are never (or very rarely) taken in May or the early part of July, in the latter part of November, or the early part of January. But a spring spawning certainly occurs in the latter part of January, in February, in March, and in April; and an autumn spawning in the latter part of July, in August, September, October, and even as late as November. Taking all parts of the British coast together, February and March are the great months for

[1] "Ueber das Kopfskelet von *Alepocephalus rostratus*," *Morphologisches Jahrbuch*, Bd. iv., Suppl. 1878.

the spring spawning, and August and September for the autumn spawning. It is not at all likely that the same fish spawn twice in the year ; on the contrary, the spring and the autumn shoals are probably perfectly distinct ; and if the herring, according to the hypothesis advanced above, come to maturity in a year, the shoals of each spawning season would be the fry of the twelvemonth before. However, no direct evidence can be adduced in favour of this supposition, and it would be extremely difficult to obtain such evidence." [1]

I believe that these conclusions, confirmatory of those of previous careful observers [2] are fully supported by all the evidence which has been collected, and the fact that this species of fish has two spawning seasons, one in the hottest and one in the coldest months, of the year, is very curious.

Another singular circumstance connected with the spawning of the herring is the great variety of the conditions, apart from temperature, to which the fish adapts itself in performing this function. On our own coasts, herrings spawn in water of from ten to twenty fathoms, and even at greater depths, and in a sea of full oceanic saltness. Nevertheless herrings spawn just as freely, not only in the narrows of the Baltic, such as the Great Belt, in which the water is not half as salt as it is in the North Sea and in the Atlantic, but even in such long inlets as the Schlei in Schleswig, the water of which is quite drinkable and is inhabited by freshwater fish. Here the herrings deposit their eggs in two or three feet of water ; and they are found along with the eggs of freshwater fish, sticking in abundance to such freshwater plants as *Potamogeton*.

Nature seems thus to offer us a hint as to the way in which a fish like the shad, which is so closely allied to the herring, has acquired the habit of ascending rivers to deposit its eggs in purely fresh water.

If a full female herring is gently squeezed over a vessel of sea-water, the eggs will rapidly pour out and sink to the bottom, to which they immediately adhere with so much tenacity that, in half an hour, the vessel may be inverted without their dropping out. When spawning takes place naturally the eggs fall to the bottom and attach themselves in a similar fashion. But, at this time, the assembled fish dart wildly about, and the water becomes cloudy with the shed fluid of the milt. The eggs thus become fecundated as they fall, and

[1] "Report of the Royal Commission on the operation of the Acts relating to Trawling or Herrings on the Coast of Scotland (1863)," p. 28.

[2] Brandt and Ratzeburg, for example, in 1833 strongly asserted that the herring has two spawning seasons.

the development of the young within the ova sticking to the bottom commences at once.

The first definite and conclusive evidence as to the manner in which herring spawn is attached and becomes developed that I know of, was obtained by Prof. Allman and Dr. MacBain in 1862,[1] in the Firth of Forth. By dredging in localities in which spent herring were observed on the 1st of March, Professor Allman brought up spawn in abundance at a depth of fourteen to twenty-one fathoms. It was deposited on the surface of the stones, shingle, and gravel, and on old shells and coarse shell-sand, and even on the shells of small living crabs and other crustacea, adhering tenaciously to whatever it had fallen on. No spawn was found in any other part of the Forth; but it continued to be abundant on both the east and the west sides of the Isle of Man up to the 13th of March, at which time the incubation of the ovum was found to be completed in a great portion of the spawn, and the embryos had become free. On the 25th scarcely a trace of spawn could be detected, and nearly the whole of the adult fish had left the Forth.

Prof. Allman draws attention to the fact "that the deposit of spawn, as evidenced by the appearance of spent herrings, did not take place till about sixty-five days after the appearance of the herring in the Firth," and arrives at the conclusion that "the incubation probably continues during a period of between twenty-five to thirty days," adding however that the estimate must for the present be regarded as only approximative. It was on this and other evidence that we based our conclusion that the eggs of the herring "are hatched in at most from two to three weeks after deposition."

Within the last few years a clear light has been thrown upon this question by the labours of the West Baltic Fishery Commission, to which I have so often had occasion to refer.[2] It has been found that artificial fecundation is easily practised, and that the young fish may be kept in aquaria for as long as five months. Thus, a great body of accurate information, some of it of a very unexpected character, has been obtained respecting the development of the eggs, and the early condition of the young herring.

[1] "Report of the Royal Commission on the Operation of the Acts relating to Trawling for Herring on the Coast of Scotland, 1863."

[2] See the four valuable memoirs, Kupffer, "Ueber Laichen und Entwickelung des Herings in der westlichen Ostsee"; *Idem*, "Die Entwickelung des Herings im Ei"; Meyer, "Beobachtungen über den Wachsthum des Herings"; Heincke, "Die Varietäten des Herings," which are contained in the *Jahresbericht der Commission in Kiel für* 1874-75-76—1878. Widegren's essay "On the Herring," 1871, translated from the Danish in U.S. Commission Reports, 1873—75, also contains important information.

It turns out that, as is the case with other fishes, the period of incubation is closely dependent upon warmth. When the water has a temperature of 53° Fahrenheit, the eggs of the herring hatch in from 6—8 days; the average being seven days. And this is a very interesting fact when we bear in mind the conclusion to which the inquiries of the Dutch meteorologists, and, more lately, those of the Scottish Meteorological Society appear to tend, namely, that the shoals prefer water of about 55°. At 50° Fahrenheit, the period of incubation is lengthened to eleven days; at 46° to fifteen days; and at 38° it lasts forty days. As the Forth is usually tolerably cool in the month of March, it is probable that Prof. Allman's estimate comes very near the truth for the particular case which he investigated.

The young, when they emerge from the egg, are from one-fifth to one-third of an inch in length, and so extremely unlike the adult herring that they may properly be termed larvæ. They have enormous eyes and an exceedingly slender body, with a yelk bag protruding from its forepart. The skeleton is in a very rudimentary condition; there are no ventral fins; and instead of separate dorsal, caudal, and anal fins, there is one continuous fin extending from the head along the back, round the tail, and then forwards to the yelk bag. The intestine is a simple tube, ciliated internally; there is no air-bladder, and no branchiæ are yet developed. The heart is a mere contractile vessel, and the blood is a clear fluid without corpuscles. At first the larvæ do not feed, but merely grow at the expense of the yelk, which gradually diminishes.

Within three or four days after hatching, the length has increased by about half the original dimensions, the yelk has disappeared, the cartilaginous skeleton appears, and the heart becomes divided into its chambers; but the young fish attains nearly double its first length before blood corpuscles are visible.

By the time the larva is two-thirds of an inch long (a length which it attains one month after hatching), the primitive median fin is separated into dorsal, caudal, and anal divisions, but the ventral fins have not appeared. About this period the young animal begins to feed on small crustacea; and it grows so rapidly that, at two months, it is 1¼ inch long, and, at three months, has attained a length of about two inches.

Nearly up to this stage the elongated scaleless little fish retains its larval proportions; but, in the latter part of the third month, the body rapidly deepens, the scales begin to appear, and the larva passes into the "imago" state—that is, assumes the form and

proportions of the adult, though it is not more than two inches long. After this, it goes on growing at the same rate (11 millimetres, or nearly half an inch) per month, so that, at six months old, it is as large as a moderate-sized sprat.

The well-known "whitebait" of the Thames consists, so far as I have seen, almost exclusively of herrings, under six months old, and as the average size of whitebait increases, from March and April onwards, until they become suspiciously like sprats in the late summer, it may be concluded that they are the progeny of herrings which spawned, early in the year, in the neighbourhood of the estuary of the Thames, up which these dainty little fish have wandered. Whether it is the general habit of young herring, even of those which are spawned in deep water, to migrate into the shallow parts of the sea, or even into completely fresh waters, when such are accessible, is unknown.

In the Report on Trawling (1863) we observe :—

"It is extremely difficult to obtain any satisfactory evidence as to the length of time which the herring requires to pass from the embryonic to the adult or *full* condition. Of the fishermen who gave any opinion on this subject, some considered that a herring takes three, and others that it requires seven, years to attain the full or spawning condition ; others frankly admitted that they knew nothing about the matter ; and it was not difficult, by a little cross-examination, to satisfy ourselves that they were all really in this condition, however strongly they might hold by their triennial or septennial theories. Mr. Yarrell and Mr. Mitchell suppose with more reason that herring attain to full size and maturity in about eighteen months.

"It does not appear, however, that there is any good evidence against the supposition that the herring reaches its spawning condition in one year. There is much reason to believe that the eggs are hatched in, at most, from two to three weeks after deposition, and that in six to seven weeks more (that is at most ten weeks from the time of laying the eggs) the young have attained three inches in length. Now it has been ascertained that a young smolt may leave a river and return to it again in a couple of months increased in bulk eight or tenfold, and as a herring lives on very much the same food as a smolt, it appears possible that it should increase in the same rapid ratio. Under these circumstances nine months would be ample time for it to enlarge from three to ten or eleven inches in length. It may be fairly argued, however, that it is not very safe to reason analogically from the rate of growth of one species of fish to that of another ; and

it may be well to leave the question whether the herring attains its maturity in twelve, fifteen or sixteen months open, in the tolerably firm assurance that the period last named is the maximum."

On comparing these conclusions with the results of the careful observations of the Baltic Commissioners, it appears that we somewhat over-estimated the rate of growth of the young herring, and that the view taken by Yarrell and Mitchell is more nearly correct. For supposing that the rate of growth after six months continues the same as before, a herring twelve months old will be nearly six inches long, and at eighteen months eight or nine inches. But full herrings may be met with little more than seven inches long, and they are very commonly found not more than nine inches in length.[1]

Fishermen distinguish four states of the herring. Fry or sile, when not larger than sprats; maties, when larger than this, with undeveloped roe or milt; full fish, with largely developed roe or milt; and spent or shotten fish, which have recently spawned.

Herring fry of the size of sprats are distinguished from full fish not merely by their size, but in addition, by the very slight development of the milt or roe, and by the accumulation of fat in the abdominal cavity. Bands of fat are found in the mesentery alongside the intestine, filling up the interspaces between the pyloric cæca.

Maties (the name[2] of which is a corruption of the Dutch word for a maiden) resemble the fry in these particulars; but, if they are well fed, the deposit of fatty and other nutritive matter takes place, not only about the abdominal viscera, but also beneath the skin and in the interstices of the flesh. Indeed, when nourishment is abundant, this infiltration of the flesh with fat may go so far that the fish cannot readily be preserved and must be eaten fresh. The singularly delicate Loch Fyne herrings are in this condition early in the season. When the small crustaceans, on which the maties chiefly feed, are extremely abundant the fish gorge themselves with them to such an extent that the conical crop becomes completely distended, and the Scotch fishermen give them the name of

[1] Ljungman ("Preliminary Report on Herrings and Herring Fisheries on the West Coast of Sweden," translated in U.S. Commission Report, 1873-5) speaks of full herrings ready to spawn only 100-110 mm. (4 to 4½ in) long, as observed by himself.

[2] "Halecum intestina, non modo multa gaudere obesitate, sed et totum corpus eo adeo esse impletum ut aliquando, cum discinditur, pinguedo ex cultro defluat, et præsertim eo quidem tempore ubi halecum lactes aut ova crescere primum incipiunt, unde nostrates eos *Maatgens-Haringen* dicere-solent."—A. v. Leeuwenhoek, "Arcana Naturæ," Ep. xcvii. (1696).

Leeuwenhoek also mentions having heard of "gut-pock" herrings from Scotch fishermen.

"gut-pock herrings," as much as to say pouch-gutted fish, and an absurd notion is current that these herrings are diseased. However, the "gut-pock" herrings differ from the rest only in having their pouch full instead of empty, as it commonly is.

As the fish passes from the matie to the full condition, the milt and roe begin to grow at the expense of the nutriment thus stored up; and, as these organs become larger and occupy more and more space in the abdominal cavity, the excess of nutritious substance is transferred to them. The fatty deposit about the intestine and pyloric cæca gradually disappears and the flesh becomes poorer. It would appear that by degrees the fish ceased to feed at all. At any rate, there is usually no food in the stomach of a herring which approaches maturity. In all these respects there is the closest resemblance between the history of the herring and that of other fishes such as the salmon—the parr corresponding to the herring fry or sile, the grilse and the "clean fish" of larger size to the maties.

At length spawning takes place, the accumulated nutrition, transformed into eggs or spermatic fluid, is expelled, and the fish is left in that lean and depauperated state which makes a "shotten herring" proverbial. In this condition it answers to the salmon "kelt," and the milt or roe are now shrunk and flaccid and can be blown up with air like empty bags. If the spent fish escapes its myriad enemies, it doubtless begins to feed again and once more passes into the matie state in preparation for the next breeding season. But the nature of this process of recuperation has yet to be investigated.

When they have reached the matie stage, the herrings, which are at all times gregarious, associate together in conspicuous assemblages, which are called shoals. These are sometimes of prodigious extent—indeed eight or nine miles in length, two or three in breadth, with an unknown depth, are dimensions which are credibly asserted to be sometimes attained. In these shoals the fish are closely packed, like a flock of sheep straying slowly along a pasture, and it is probably quite safe to assume that there is at least one fish for every cubic foot of water occupied by the shoal. If this be so, every square mile of such a shoal, supposing it to be three fathoms deep, must contain more than 500,000,000 herrings. And when it is considered that many shoals approach the coasts, not only of our own islands, but of Scandinavia and the Baltic, and of Eastern North America, every spring and autumn, the sum total of the herrings which people our seas surpasses imagination.

If you read any old and some new books on the natural history of

the herring, you will find a wonderful story about the movements of these shoals. How they start from their home in the Polar Seas, and march south as a great armada which splits into minor divisions —one destined to spawn on the Scandinavian, and one on our own shores; and how, having achieved this spawning raid, the spent fish make their way as fast as they can back to their Arctic refuge, there to repair their exhausted frames in domestic security. This story was started in the last century, and was unfortunately adopted and disseminated by our countryman Pennant. But there is not the least proof that anything of the kind takes place, and the probabilities are wholly against it. It is, for example, quite irreconcilable with the fact that herring are found in cods' stomachs all the year round. And the circumstance to which I have already adverted, that practised eyes distinguish local breeds of herrings, though it does not actually negative the migration hypothesis, is very much against it. The supposition that the herring spawn in the north in the early spring, and in the south in the autumn, fitted very well into the notion that the vanguard of the migrating body of herrings occupied the first spawning ground it reached, and obliged the rest of the horde to pass on. But, as a matter of fact, the northern herrings, like the southern, have two spawning times; or perhaps it would be more correct to say that the spawning time extends from autumn to spring, and has two maxima—one in August-September, and one in February-March.

Finally, there is no evidence that herrings are to be met with in the extreme north of their range, at other times, or in greater abundance, than they are to be found elsewhere.

In the matter of its migration, as in other respects, the herring compares best with the salmon. The ordinary habitation of both fishes is no doubt the moderately deep portion of the sea. It is only as the breeding time draws near that the herrings (not yet advanced beyond the matie state) gather together towards the surface and approach the land in great shoals for the purpose of spawning in relatively or absolutely shallow water. In the case of the herring of the Schlei we have almost the connecting link between the exclusively marine ordinary herring and the river ascending salmon.

The records of the herring fisheries are, for the most part, neither very ancient nor (with the exception of those of the Scotch Fishery Board) very accurately kept; and, from the nature of the case, they can only tell us whether the fish in any given year were readily taken or not, and that may have very little to do with the actual strength of the shoals.

However, there is historical evidence that, long before the time of

Henry the First, Yarmouth was frequented by herring fishers. This means, that for eight centuries, herrings have been fished on the English coast, and I cannot make out, taking one year with another, in recent times, that there has been any serious fluctuation in their numbers. The number captured must have enormously increased in the last two centuries, and yet there is no sign of diminution of the shoals.

In 1864, we had to listen to dolorous prophecies of the coming exhaustion of the Scotch herring fisheries. The fact that the returns showed no falling off was ascribed to the improvement of the gear and methods of fishing, and to the much greater distances to which the fishermen extend their operations. Yet what has really happened? The returns of subsequent years prove, not only that the average cure of the decade 1869–78 was considerably greater than that of the previous decade, but that the years 1874 and 1880 are absolutely without parallel in the annals of the Scotch herring fishery, a million barrels having been cured in the first of these years, and a million and a half in 1880. In the decade 1859–68, the average was 670,000 barrels, and the highest 830,000.

In dealing with questions of biology, *a priori* reasoning is somewhat risky, and if any one tells me "it stands to reason" that such and such things must happen, I generally find reason to doubt the safety of his standing.

It is said that "it stands to reason" that destruction on such a prodigious scale as that effected by herring fishers must tell on the supply. But again let us look at the facts. It is said that 2,500,000,000, or thereabouts, of herrings are every year taken out of the North Sea and the Atlantic. Suppose we assume the number to be 3,000,000,000 so as to be quite safe. It is a large number undoubtedly, but what does it come to? Not more than that of the herrings which may be contained in one shoal, if it covers half a dozen square miles—and shoals of much larger size are on record. It is safe to say that, scattered through the North Sea and the Atlantic, at one and the same time, there must be scores of shoals, any one of which would go a long way towards supplying the whole of man's consumption of herrings. I do not believe that all the herring fleets taken together destroy 5 per cent. of the total number of herrings in the sea in any year, and I see no reason to swerve from the conviction my colleagues and I expressed in our Report, that their destructive operations are totally insignificant when compared with those which, as a simple calculation shows, must regularly and normally go on.

Suppose that every mature female herring lays 10,000 eggs, that the fish are not interfered with by man, and that their numbers remain approximately the same year after year, it follows that 9998 of the progeny of every female must be destroyed before they reach maturity. For if more than two out of the 10,000 escape destruction, the number of herrings will be proportionately increased. Or in other words, if the average strength of the shoals which visit a given locality is to remain the same year by year, many thousand times the number contained in those shoals must be annually destroyed. And how this enormous amount of destruction is effected will be obvious to any one who considers the operations of the fin-whales, the porpoises, the gannets, the gulls, the codfish, and the dogfish, which accompany the shoals and perennially feast upon them ; to say nothing of the flat-fish, which prey upon the newly deposited spawn ; or of the mackerel, and the innumerable smaller enemies which devour the fry in all stages of their development. It is no uncommon thing to find five or six—nay, even ten or twelve—herrings in the stomach of a codfish,[1] and, in 1863, we calculated that the whole take of the great Scotch herring fisheries is less than the number of herrings which would in all probability have been consumed by the codfish captured in the same waters if they had been left in the sea.[2]

Man, in fact, is but one of a vast co-operative society of herring-catchers, and the larger the share he takes, the less there is for the rest of the company. If man took none, the other shareholders would have a larger dividend, and would thrive and multiply in proportion, but it would come to pretty much the same thing to the herrings.

As long as the records of history give us information, herrings appear to have abounded on the east coast of the British Islands, and there is nothing to show, so far as I am aware, that, taking an average of years, they were ever either more or less numerous than they are at present. But in remarkable contrast with this constancy, the shoals of herrings have elsewhere exhibited a strange capriciousness—visiting a given locality for many years in great numbers, and then suddenly disappearing. Several well-marked examples of this fickleness are recorded on the west

[1] In his valuable Report on the Salt Water Fisheries of Norway (1877), Prof. Sars expresses the belief that full-grown codfishes feed chiefly, if not exclusively, on herrings.

[2] In 1879 rather more than 5,000,000 cod, ling, and hake, were taken by the Scottish fishermen. Allowing each only two herrings a day, these fishes would have consumed more than three thousand five hundred millions of herrings in a year. As to the Norwegian fisheries, 20,000,000 codfishes are said to taken annually by the Lofoden fishermen alone.

coast of Scotland; but the most remarkable is that furnished by the fisheries of Bohüslan, a province which lies on the south-western shore of the Scandinavian peninsula. Here a variety known as the "old" or "great" herring, after being so extremely abundant, for about sixty years, as to give rise to a great industry, disappeared in the year 1808, as suddenly as they made their appearance, and have not since been seen in any number.

The desertion of their ordinary grounds by the herring has been attributed to all imaginable causes, from fishing on a Sunday to the offence caused to the fish by the decomposing carcases of their brethren, dropped upon the bottom out of the nets. The truth is that absolutely nothing is known on the subject; and that little is likely to be known, until careful and long-continued meteorological and zoological observations have furnished definite information respecting the changes which take place in the temperature of the sea, and the distribution of the pelagic crustacea which constitute the chief food of the herring shoals. The institution of systematic observations of this kind is an object of international importance, towards the attainment of which the British, Scandinavian, Dutch, and French Governments might wisely make a combined effort.

A great fuss has been made about trawlers working over the spawning grounds of the herring. "It stands to reason," we were told, that they must destroy an immense quantity of the spawn. Indeed this looked so reasonable, that we inquired very particularly into a case of the alleged malpractice which was complained of on the east coast of Scotland near Pittenweem. Off this place, there is a famous spawning ground known as the Traith hole, and we were told that the trawlers worked vigorously over the spot immediately after the herring had deposited their spawn. Of course our first proceeding was to ask the trawlers why they took the trouble of doing what looked like wanton mischief. And their answer was reasonable enough. It was to catch the prodigious abundance of flat-fish which were to be found on the Traith at that time. Well, then, why did the flat-fish congregate there? Simply to feed on herring eggs, which seem to be a sort of flat-fishes' caviare. The stomachs of the flat-fish brought up by the trawl were, in fact, crammed with masses of herring eggs.

Thus every flat-fish caught by the trawl was an energetic destroyer of herring arrested in his career. And the trawling, instead of injuring the herring, captured and removed hosts of their worst enemies. That is how "it stood to reason" when one got to the bottom of the matter.

I do not think that any one who looks carefully into the subject will arrive at any other conclusion than that reached by my colleagues and myself: namely, that the best thing for Governments to do in relation to the herring fisheries, is to let them alone, except in so far as the police of the sea is concerned. With this proviso, let people fish how they like, as they like, and when they like. At present, I must repeat the conviction we expressed so many years ago, that there is not a particle of evidence that anything man does has an appreciable influence on the stock of herrings. It will be time to meddle, when any satisfactory evidence that mischief is being done is produced.

XXVIII

THE CONNECTION OF THE BIOLOGICAL SCIENCES WITH MEDICINE

Nature, August 11th, 1881, *vol. xxiv., pp.* 342–346. (*Address at the International Medical Congress.*)

THE great body of theoretical and practical knowledge which has been accumulated by the labours of some eighty generations, since the dawn of scientific thought in Europe, has no collective English name to which an objection may not be raised; and I use the term "medicine" as that which is least likely to be misunderstood; though, as every one knows, the name is commonly applied, in a narrower sense, to one of the chief divisions of the totality of medical science.

Taken in this broad sense, "medicine" not merely denotes a kind of knowledge; but it comprehends the various applications of that knowledge to the alleviation of the sufferings, the repair of the injuries, and the conservation of the health, of living beings. In fact, the practical aspect of medicine so far dominates over every other, that the "Healing Art" is one of its most widely received synonyms. It is so difficult to think of medicine otherwise than as something which is necessarily connected with curative treatment, that we are apt to forget that there must be, and is, such a thing as a pure science of medicine—a "pathology" which has no more necessary subservience to practical ends than has zoology or botany.

The logical connection between this purely scientific doctrine of disease, or pathology, and ordinary biology, is easily traced. Living matter is characterised by its innate tendency to exhibit a definite series of the morphological and physiological phenomena which constitute organisation and life. Given a certain range of conditions, and these phenomena remain the same, within narrow limits, for each

kind of living thing. They furnish the normal and typical characters of the species; and, as such, they are the subject matter of ordinary biology.

Outside the range of these conditions, the normal course of the cycle of vital phenomena is disturbed; abnormal structure makes its appearance, or the proper character and mutual adjustment of the functions cease to be preserved. The extent and the importance of these deviations from the typical life may vary indefinitely. They may have no noticeable influence on the general well-being of the economy, or they may favour it. On the other hand, they may be of such a nature as to impede the activities of the organism, or even to involve its destruction.

In the first case, these perturbations are ranged under the wide and somewhat vague category of "variations"; in the second, they are called lesions, states of poisoning, or diseases; and, as morbid states, they lie within the province of pathology. No sharp line of demarcation can be drawn between the two classes of phenomena. No one can say where anatomical variations end and tumours begin, nor where modification of function, which may at first promote health, passes into disease. All that can be said is, that whatever change of structure or function is hurtful belongs to pathology. Hence it is obvious that pathology is a branch of biology; it is the morphology, the physiology, the distribution, the ætiology of abnormal life.

However obvious this conclusion may be now, it was nowise apparent in the infancy of medicine. For it is a peculiarity of the physical sciences, that they are independent in proportion as they are imperfect; and it is only as they advance that the bonds which really unite them all become apparent. Astronomy had no manifest connection with terrestrial physics before the publication of the "Principia"; that of chemistry with physics is of still more modern revelation; that of physics and chemistry, with physiology, has been stoutly denied within the recollection of most of us, and perhaps still may be.

Or, to take a case which affords a closer parallel with that of medicine. Agriculture has been cultivated from the earliest times; and, from a remote antiquity, men have attained considerable practical skill in the cultivation of the useful plants, and have empirically established many scientific truths concerning the conditions under which they flourish. But it is within the memory of many of us that chemistry on the one hand, and vegetable physiology on the other, attained a stage of development such that they were able

to furnish a sound basis for scientific agriculture. Similarly, medicine took its rise in the practical needs of mankind. At first, studied without reference to any other branch of knowledge, it long maintained, indeed still to some extent maintains, that independence. Historically, its connection with the biological sciences has been slowly established, and the full extent and intimacy of that connection are only now beginning to be apparent. I trust I have not been mistaken in supposing that an attempt to give a brief sketch of the steps by which a philosophical necessity has become a historical reality, may not be devoid of interest, possibly of instruction, to the members of this great Congress, profoundly interested as all are in the scientific development of medicine.

The history of medicine is more complete and fuller than that of any other science, except perhaps astronomy; and if we follow back the long record as far as clear evidence lights us, we find ourselves taken to the early stages of the civilisation of Greece. The oldest hospitals were the temples of Æsculapius; to these Asclepeia, always erected on healthy sites, hard by fresh springs and surrounded by shady groves, the sick and the maimed resorted to seek the aid of the god of health. Votive tablets or inscriptions recorded the symptoms, no less than the gratitude, of those who were healed; and, from these primitive clinical records, the half-priestly, half-philosophic, caste of the Asclepiads compiled the data upon which the earliest generalisations of medicine, as an inductive science, were based.

In this state, pathology, like all the inductive sciences at their origin, was merely natural history; it registered the phenomena of disease, classified them, and ventured upon a prognosis, wherever the observation of constant co-existences and sequences suggested a rational expectation of the like recurrence under similar circumstances.

Further than this, it hardly went. In fact, in the then state of knowledge and in the condition of philosophical speculation at that time, neither the causes of the morbid state, nor the *rationale* of treatment, were likely to be sought for as we seek for them now. The anger of a God was a sufficient reason for the existence of a malady, and a dream ample warranty for therapeutic measures; that a physical phenomenon must needs have a physical cause was not the implied or expressed axiom that it is to us moderns.

The great man, whose name is inseparably connected with the foundation of medicine, Hippocrates, certainly knew very little, indeed practically nothing, of anatomy or physiology; and he would probably have been perplexed, even to imagine the possibility of a connection between the zoological studies of his contemporary

Democritus, and medicine. Nevertheless, in so far as he, and those who worked before and after him, in the same spirit, ascertained, as matters of experience, that a wound, or a luxation, or a fever, presented such and such symptoms, and that the return of the patient to health was facilitated by such and such measures, they established laws of nature, and began the construction of the science of pathology.—All true science begins with empiricism—though all true science is such exactly in so far as it strives to pass out of the empirical stage into that of the deduction of empirical from more general truths. Thus, it is not wonderful that the early physicians had little or nothing to do with the development of biological science; and, on the other hand, that the early biologists did not much concern themselves with medicine. There is nothing to show that the Asclepiads took any prominent share in the work of founding anatomy, physiology, zoology, and botany. Rather do these seem to have sprung from the early philosophers, who were essentially natural philosophers, animated by the characteristically Greek thirst for knowledge as such. Pythagoras, Alcmeon, Democritus, Diogenes of Apollonia, are all credited with anatomical and physiological investigation; and though Aristotle is said to have belonged to an Asclepiad family, and not improbably owed his taste for anatomical and zoological inquiries to the teachings of his father, the physician Nicomachus, the "Historia Animalium," and the treatise "De Partibus Animalium," are as free from any allusion to medicine as if they had issued from a modern biological laboratory.

It may be added, that it is not easy to see in what way it could have benefited a physician of Alexander's time to know all that Aristotle knew on these subjects. His human anatomy was too rough to avail much in diagnosis, his physiology was too erroneous to supply data for pathological reasoning. But when the Alexandrian school, with Erasistratus and Herophilus at their head, turned to account the opportunities of studying human structure, afforded to them by the Ptolemies, the value of the large amount of accurate knowledge thus obtained to the surgeon for his operations, and to the physician for his diagnosis of internal disorders, became obvious, and a connection was established between anatomy and medicine, which has ever become closer and closer. Since the revival of learning, surgery, medical diagnosis, and anatomy have gone hand in hand. Morgagni called his great work, "De sedibus et causis morborum per anatomen indagatis," and not only showed the way to search out the localities and the causes of disease by anatomy, but himself travelled wonderfully far upon the road. Bichat, discriminat-

ing the grosser constituents of the organs and parts of the body, one from another, pointed out the direction which modern research must take; until, at length, histology, a science of yesterday, as it seems to many of us, has carried the work of Morgagni as far as the microscope can take us, and has extended the realm of pathological anatomy to the limits of the invisible world.

Thanks to the intimate alliance of morphology with medicine, the natural history of disease has, at the present day, attained a high degree of perfection. Accurate regional anatomy has rendered practicable the exploration of the most hidden parts of the organism, and the determination during life of morbid changes in them; anatomical and histological post-mortem investigations have supplied physicians with a clear basis upon which to rest the classification of diseases, and with unerring tests of the accuracy or inaccuracy of their diagnoses.

If men could be satisfied with pure knowledge, the extreme precision with which, in these days, a sufferer may be told what is happening and what is likely to happen, even in the most recondite parts of his bodily frame, should be as satisfactory to the patient, as it is to the scientific pathologist who gives him the information. But I am afraid it is not; and even the practising physician, while no wise underestimating the regulative value of accurate diagnosis, must often lament that so much of his knowledge rather prevents him from doing wrong, than helps him to do right.

A scorner of physic once said that nature and disease may be compared to two men fighting, the doctor to a blind man with a club, who strikes into the *mêlé*, sometimes hitting the disease, and sometimes hitting nature. The matter is not mended if you suppose the blind man's hearing to be so acute that he can register every stage of the struggle and pretty clearly predict how it will end. He had better not meddle at all, until his eyes are opened—until he can see the exact position of the antagonists, and make sure of the effect of his blows. But that which it behoves the physician to see, not indeed with his bodily eye, but with clear intellectual vision, is a process, and the chain of causation involved in that process. Disease, as we have seen, is a perturbation of the normal activities of a living body; and it is, and must remain, unintelligible, so long as we are ignorant of the nature of these normal activities.—In other words, there could be no real science of pathology, until the science of physiology had reached a degree of perfection unattained, and indeed unattainable, until quite recent times.

So far as medicine is concerned, I am not sure that physiology

such as it was down to the time of Harvey, might as well not have existed. Nay, it is perhaps no exaggeration to say, that within the memory of living men, justly renowned practitioners of medicine and surgery knew less physiology than is now to be learned from the most elementary text-book; and, beyond a few broad facts, regarded what they did know, as of extremely little practical importance. Nor am I disposed to blame them for this conclusion; physiology must be useless, or worse than useless, to pathology, so long as its fundamental conceptions are erroneous.

Harvey is often said to be the founder of modern physiology; and there can be no question that the elucidations of the function of the heart, of the nature of the pulse, and of the course of the blood, put forth in the ever-memorable little essay "De motu cordis," directly worked a revolution in men's views of the nature and of the concatenation of some of the most important physiological processes among the higher animals; while, indirectly, their influence was perhaps even more remarkable.

But, though Harvey made this signal and perennially important contribution to the physiology of the moderns, his general conception of vital processes was essentially identical with that of the ancients; and, in the "Exercitationes de generatione," and notably in the singular chapter "De calido innato," he shows himself a true son of Galen and of Aristotle.

For Harvey, the blood possesses powers superior to those of the elements; it is the seat of a soul which is not only vegetative, but also, sensitive and motor. The blood maintains and fashions all parts of the body, "idque summâ cum providentiâ et intellectu in finem certum agens, quasi ratiocinio quodam uteretur."

Here is the doctrine of the "pneuma," the product of the philosophical mould into which the animism of primitive men ran in Greece, in full force. Nor did its strength abate for long after Harvey's time. The same ingrained tendency of the human mind to suppose that a process is explained when it is ascribed to a power of which nothing is known except that it is the hypothetical agent of the process, gave rise in the next century to the animism of Stahl; and, later, to the doctrine of a vital principle, that "asylum ignorantiæ" of physiologists, which has so easily accounted for everything and explained nothing, down to our own times.

Now the essence of modern, as contrasted with ancient, physiological science, appears to me to lie in its antagonism to animistic hypotheses and animistic phraseology. It offers physical explanations of vital phenomena, or frankly confesses that it has none to offer.

And so far as I know, the first person who gave expression to this modern view of physiology, who was bold enough to enunciate the proposition that vital phenomena, like all the other phenomena of the physical world, are, in ultimate analysis, resolvable into matter and motion, was René Descartes.

The fifty-four years of life of this most original and powerful thinker are widely overlapped, on both sides, by the eighty of Harvey, who survived his younger contemporary by seven years, and takes pleasure in acknowledging the French philosopher's appreciation of his great discovery.

In fact, Descartes accepted the doctrine of the circulation as propounded by "Hervæus, médecin d'Angleterre," and gave a full account of it in his first work, the famous "Discours de la Méthode," which was published in 1637, only nine years after the exercitation "De motu cordis"; and, though differing from Harvey in some important points (in which it may be noted, in passing, Descartes was wrong and Harvey right), he always speaks of him with great respect. And so important does the subject seem to Descartes, that he returns to it in the "Traité des Passions," and in the "Traité de l'Homme."

It is easy to see that Harvey's work must have had a peculiar significance for the subtle thinker to whom we owe both the spiritualistic and the materialistic philosophies of modern times. It was in the very year of its publication, 1628, that Descartes withdrew into that life of solitary investigation and meditation of which his philosophy was the fruit. And, as the course of his speculations led him to establish an absolute distinction of nature between the material and the mental worlds, he was logically compelled to seek for the explanation of the phenomena of the material world within itself; and having allotted the realm of thought to the soul, to see nothing but extension and motion in the rest of nature. Descartes uses "thought" as the equivalent of our modern term "consciousness." Thought is the function of the soul, and its only function. Our natural heat and all the movements of the body, says he, do not depend on the soul. Death does not take place from any fault of the soul, but only because some of the principal parts of the body become corrupted. The body of a living man differs from that of a dead man in the same way as a watch or other automaton (that is to say, a machine which moves of itself) when it is wound up and has in itself the physical principle of the movements which the mechanism is adapted to perform, differs from the same watch, or other machine, when it is broken and the physical principle of its movement no longer exists. All the actions which are common to us and the

lower animals depend only on the conformation of our organs and the course which the animal spirits take in the brain, the nerves, and the muscles; in the same way as the movement of a watch is produced by nothing but the force of its spring and the figure of its wheels and other parts.

Descartes' Treatise on Man is a sketch of human physiology in which a bold attempt is made to explain all the phenomena of life, except those of consciousness, by physical reasonings. To a mind turned in this direction, Harvey's exposition of the heart and vessels as a hydraulic mechanism must have been supremely welcome.

Descartes was not a mere philosophical theorist, but a hard-working dissector and experimenter, and he held the strongest opinion respecting the practical value of the new conception which he was introducing. He speaks of the importance of preserving health, and of the dependence of the mind on the body being so close that perhaps the only way of making men wiser and better than they are, is to be sought in medical science. "It is true," says he, "that as medicine is now practised, it contains little that is very useful; but without any desire to depreciate, I am sure that there is no one, even among professional men, who will not declare that all we know is very little as compared with that which remains to be known; and that we might escape an infinity of diseases of the mind, no less than of the body, and even perhaps from the weakness of old age, if we had sufficient knowledge of their causes, and of all the remedies with which nature has provided us."[1] So strongly impressed was Descartes with this, that he resolved to spend the rest of his life in trying to acquire such a knowledge of nature as would lead to the construction of a better medical doctrine.[2] The anti-Cartesians found material for cheap ridicule in these aspirations of the philosopher; and it is almost needless to say that, in the thirteen years which elapsed between the publication of the "Discours" and the death of Descartes, he did not contribute much to their realisation. But, for the next century, all progress in physiology took place along the lines which Descartes laid down.

The greatest physiological and pathological work of the seventeenth century, Borelli's treatise "De motu animalium," is, to all intents and purposes, a development of Descartes' fundamental conception; and the same may be said of the physiology and pathology of Boerhaave, whose authority dominated in the medical world of the first half of the eighteenth century.

[1] "Discours de la Méthode," 6e partie, Ed. Cousin, p. 193.
[2] *Ibid.* pp. 193 and 211.

With the origin of modern chemistry, and of electrical science in the latter half of the eighteenth century, aids in the analysis of the phenomena of life, of which Descartes could not have dreamed, were offered to the physiologist. And the greater part of the gigantic progress which has been made in the present century is a justification of the prevision of Descartes. For it consists, essentially, in a more and more complete resolution of the grosser organs of the living body into physico-chemical mechanisms.

"I shall try to explain our whole bodily machinery in such a way, that it will be no more necessary for us to suppose that the soul produces such movements as are not voluntary, than it is to think that there is in a clock a soul which causes it to show the hours."[1] These words of Descartes might be appropriately taken as a motto by the author of any modern treatise on physiology.

But, though, as I think, there is no doubt that Descartes was the first to propound the fundamental conception of the living body as a physical mechanism, which is the distinctive feature of modern, as contrasted with ancient physiology, he was misled by the natural temptation to carry out, in all its details, a parallel between the machines with which he was familiar, such as clocks and pieces of hydraulic apparatus, and the living machine. In all such machines there is a central source of power, and the parts of the machine are merely passive distributors of that power. The Cartesian school conceived of the living body as a machine of this kind; and herein they might have learned from Galen, who, whatever ill use he may have made of the doctrine of "natural faculties," nevertheless had the great merit of perceiving that local forces play a great part in physiology.

The same truth was recognised by Glisson, but it was first prominently brought forward in the Hallerian doctrine of the "vis insita" of muscles. If muscle can contract without nerve, there is an end of the Cartesian mechanical explanation of its contraction by the influx of animal spirits.

The discoveries of Trembley tended in the same direction. In the freshwater *Hydra*, no trace was to be found of that complicated machinery upon which the performance of the functions in the higher animals was supposed to depend. And yet the hydra moved, fed, grew, multiplied, and its fragments exhibited all the powers of the whole. And, finally, the work of Caspar F. Wolff,[2] by demonstrating the fact that the growth and development of both plants and animals take place antecedently to the existence of their grosser organs, and are, in fact, the causes and not the consequences of organisation (as

[1] "De la Formation du Fœtus." [2] "Theoria Generationis," 1759.

then understood), sapped the foundations of the Cartesian physiology as a complete expression of vital phenomena.

For Wolff, the physical basis of life is a fluid, possessed of a "vis essentialis" and a "solidescibilitas," in virtue of which it gives rise to organisation; and, as he points out, this conclusion strikes at the root of the whole iatro-mechanical system.

In this country, the great authority of John Hunter exerted a similar influence; though it must be admitted that the two sibylline utterances which are the outcome of Hunter's struggles to define his conceptions are often susceptible of more than one interpretation. Nevertheless, on some points, Hunter is clear enough. For example, he is of opinion that "Spirit is only a property of matter" ("Introduction to Natural History," p. 6), he is prepared to renounce animism (*l.c.* p. 8), and his conception of life is so completely physical that he thinks of it as something which can exist in a state of combination in the food. "The aliment we take in has in it, in a fixed state, the real life; and this does not become active until it has got into the lungs; for there it is freed from its prison" ("Observations on Physiology," p. 113). He also thinks that "It is more in accord with the general principles of the animal machine to suppose that none of its effects are produced from any mechanical principle whatever; and that every effect is produced from an action in the part; which action is produced by a stimulus upon the part which acts, or upon some other part with which this part sympathises so as to take up the whole action" (*l.c.* p. 152).

And Hunter is as clear as Wolff, with whose work he was probably unacquainted, that "whatever life is, it most certainly does not depend upon structure or organisation" (*l.c.* p. 114).

Of course it is impossible that Hunter could have intended to deny the existence of purely mechanical operations in the animal body. But while, with Borelii and Boerhaave, he looked upon absorption, nutrition, and secretion, as operations effected by means of the small vessels; he differed from the mechanical physiologists, who regarded these operations as the result of the mechanical properties of the small vessels, such as the size, form, and disposition of their canals and apertures. Hunter, on the contrary, considers them to be the effect of properties of these vessels which are not mechanical but vital. "The vessels," says he, "have more of the polypus in them than any other part of the body," and he talks of the "living and sensitive principles of the arteries," and even of the "dispositions or feelings of the arteries." "When the blood is good and genuine

the sensations of the arteries, or the dispositions for sensation, are agreeable. . . . . It is then they dispose of the blood to the best advantage, increasing the growth of the whole, supplying any losses, keeping up a due succession, &c." (*l.c.* p. 133).

If we follow Hunter's conceptions to their logical issue, the life of one of the higher animals is essentially the sum of the lives of all the vessels, each of which is a sort of physiological unit, answering to a polype; and, as health is the result of the normal "action of the vessels," so is disease an effect of their abnormal action. Hunter thus stands in thought, as in time, midway between Borelli, on the one hand, and Bichat on the other.

The acute founder of general anatomy, in fact, outdoes Hunter in his desire to exclude physical reasonings from the realm of life. Except in the interpretation of the action of the sense organs, he will not allow physics to have anything to do with physiology.

"To apply the physical sciences to physiology is to explain the phenomena of living bodies by the laws of inert bodies. Now this is a false principle, hence all its consequences are marked with the same stamp. Let us leave to chemistry its affinity, to physics, its elasticity and its gravity. Let us invoke for physiology only sensibility and contractility." [1]

Of all the unfortunate dicta of men of eminent ability this seems one of the most unhappy, when we think of what the application of the methods and the data of physics and chemistry has done towards bringing physiology into its present state. It is not too much to say that one half of a modern text-book of physiology consists of applied physics and chemistry; and that it is exactly in the exploration of the phenomena of sensibility and contractility that physics and chemistry have exerted the most potent influence.

Nevertheless, Bichat rendered a solid service to physiological progress by insisting upon the fact that what we call life, in one of the higher animals, is not an indivisible unitary archæus dominating, from its central seat, the parts of the organism, but a compound result of the synthesis of the separate lives of those parts.

"All animals," says he, "are assemblages of different organs, each of which performs its function and concurs, after its fashion, in the preservation of the whole. They are so many special machines in the general machine which constitutes the individual. But each of these special machines is itself compounded of many tissues of very different natures, which in truth constitute the elements of those organs" (*l.c.* lxxix.). "The conception of a proper vitality is

[1] "Anatomie générale," i. p. liv.

applicable only to these simple tissues, and not to the organs themselves" (*l.c.* lxxxiv.).

And Bichat proceeds to make the obvious application of this doctrine of synthetic life, if I may so call it, to pathology. Since diseases are only alterations of vital properties, and the properties of each tissue are distinct from those of the rest, it is evident that the diseases of each tissue must be different from those of the rest. Therefore, in any organ composed of different tissues, one may be diseased and the other remain healthy; and this is what happens in most cases. (*l.c.* lxxxv.)

In a spirit of true prophecy, Bichat says, "we have arrived at an epoch, in which pathological anatomy should start afresh." For as the analysis of the organs had led him to the tissues as the physiological units of the organism; so, in a succeeding generation, the analysis of the tissues led to the cell as the physiological element of the tissues. The contemporaneous study of development brought out the same result, and the zoologists and botanists exploring the simplest and the lowest forms of animated beings confirmed the great induction of the cell theory. Thus the apparently opposed views, which have been battling with one another ever since the middle of the last century, have proved to be each half the truth.

The proposition of Descartes that the body of a living man is a machine, the actions of which are explicable by the known laws of matter and motion, is unquestionably largely true. But it is also true, that the living body is a synthesis of innumerable physiological elements, each of which may nearly be described, in Wolff's words, as a fluid possessed of a "vis essentialis," and a "solidescibilitas"; or in modern phrase, as protoplasm susceptible of structural metamorphosis and functional metabolism: and that the only machinery, in the precise sense in which the Cartesian school understood mechanism, is, that which co-ordinates and regulates these physiological units into an organic whole.

In fact, the body is a machine of the nature of an army, not of that of a watch, or of a hydraulic apparatus. Of this army, each cell is a soldier, an organ a brigade, the central nervous system head-quarters and field telegraph, the alimentary and circulatory system the commissariat. Losses are made good by recruits born in camp, and the life of the individual is a campaign, conducted successfully for a number of years, but with certain defeat in the long run.

The efficacy of an army, at any given moment, depends on the health of the individual soldier, and on the perfection of the machinery by which he is led and brought into action at the proper time; and,

therefore, if the analogy holds good, there can be only two kinds of diseases, the one dependent on abnormal states of the physiological units, the other on perturbation of their co-ordinating and alimentative machinery.

Hence, the establishment of the cell theory, in normal biology, was swiftly followed by a "cellular pathology," as its logical counterpart. I need not remind you how great an instrument of investigation this doctrine has proved in the hands of the man of genius to whom its development is due; and who would probably be the last to forget that abnormal conditions of the co-ordinative and distributive machinery of the body are no less important factors of disease.

Henceforward, as it appears to me, the connection of medicine with the biological sciences is clearly defined. Pure pathology is that branch of biology which defines the particular perturbation of cell life, or of the co-ordinating machinery, or of both, on which the phenomena of disease depend.

Those who are conversant with the present state of biology will hardly hesitate to admit that the conception of the life of one of the higher animals as the summation of the lives of a cell aggregate, brought into harmonious action by a co-ordinative machinery formed by some of these cells, constitutes a permanent acquisition of physiological science. But the last form of the battle between the animistic and the physical views of life is seen in the contention whether the physical analysis of vital phenomena can be carried beyond this point or not.

There are some to whom living protoplasm is a substance even such as Harvey conceived the blood to be, "summâ cum providentiâ et intellectu in finem certum agens, quasi ratiocinio quodam"; and who look, with as little favour as Bichat did, upon any attempt to apply the principles and the methods of physics and chemistry to the investigation of the vital processes of growth, metabolism, and contractility. They stand upon the ancient ways; only, in accordance with that progress towards democracy which a great political writer has declared to be the fatal characteristic of modern times, they substitute a republic formed by a few billion of "animulæ" for the monarchy of the all-pervading "anima."

Others, on the contrary, supported by a robust faith in the universal applicability of the principles laid down by Descartes, and seeing that the actions called "vital" are, so far as we have any means of knowing, nothing but changes of place of particles of matter, look to molecular physics to achieve the analysis of the living protoplasm itself into a molecular mechanism. If there is any truth in the

received doctrines of physics, that contrast between living and inert matter, on which Bichat lays so much stress, does not exist. In nature, nothing is at rest, nothing is amorphous; the simplest particle of that which men in their blindness are pleased to call "brute matter" is a vast aggregate of molecular mechanisms, performing complicated movements of immense rapidity and sensitively adjusting themselves to every change in the surrounding world. Living matter differs from other matter in degree and not in kind; the microcosm repeats the macrocosm; and one chain of causation connects the nebulous original of suns and planetary systems with the protoplasmic foundation of life and organisation.

From this point of view, pathology is the analogue of the theory of perturbations in astronomy; and therapeutics resolves itself into the discovery of the means by which a system of forces competent to eliminate any given perturbation may be introduced into the economy. And, as pathology bases itself upon normal physiology, so therapeutics rests upon pharmacology; which is, strictly speaking, a part of the great biological topic of the influence of conditions on the living organism, and has no scientific foundation apart from physiology.

It appears to me that there is no more hopeful indication of the progress of medicine towards the ideal of Descartes than is to be derived from a comparison of the state of pharmacology, at the present day, with that which existed forty years ago. If we consider the knowledge positively acquired, in this short time, of the *modus operandi* of urari, of atropia, of physostigmin, of veratria, of casca, of strychnia, of bromide of potassium, of phosphorus, there can surely be no ground for doubting that, sooner or later, the pharmacologist will supply the physician with the means of affecting, in any desired sense, the functions of any physiological element of the body. It will, in short, become possible to introduce into the economy a molecular mechanism which, like a very cunningly contrived torpedo, shall find its way to some particular group of living elements, and cause an explosion among them, leaving the rest untouched.

The search for the explanation of diseased states in modified cell life; the discovery of the important part played by parasitic organisms in the ætiology of disease; the elucidation of the action of medicaments by the methods and the data of experimental physiology; appear to me to be the greatest steps which have ever been made owards the establishment of medicine on a scientific basis. I need hardly say they could not have been made except for the advance of normal biology.

There can be no question then as to the nature or the value of

the connection between medicine and the biological sciences. There can be no doubt that the future of Pathology and of Therapeutics, and therefore that of Practical Medicine, depend upon the extent to which those who occupy themselves with these subjects are trained in the methods and impregnated with the fundamental truths of Biology.

And, in conclusion, I venture to suggest that the collective sagacity of this Congress could occupy itself with no more important question than with this: How is medical education to be arranged, so that, without entangling the student in those details of the systematist which are valueless to him, he may be enabled to obtain a firm grasp of the great truths respecting animal and vegetable life, without which, notwithstanding all the progress of scientific medicine, he will still find himself an empiric?

XXIX

THE RISE AND PROGRESS OF PALÆONTOLOGY.

Nature, September 8th, 1881, *vol. xxiv., pp.* 452-455. (*Discourse given at the York meeting of the British Association.*)

THAT application of the sciences of biology and geology which is commonly known as palæontology took its origin in the mind of the first person who, finding something like a shell or a bone naturally imbedded in gravel or in rock, indulged in speculations upon the nature of this thing which he had dug out—this "fossil"—and upon the causes which had brought it into such a position. In this rudimentary form, a high antiquity may safely be ascribed to palæontology, inasmuch as we know that, 500 years before the Christian era, the philosophic doctrines of Xenophanes were influenced by his observations upon the fossil remains exposed in the quarries of Syracuse. From this time forth, not only the philosophers, but the poets, the historians, the geographers of antiquity occasionally refer to fossils; and after the revival of learning lively controversies arose respecting their real nature. But hardly more than two centuries have elapsed since this fundamental problem was first exhaustively treated; it was only in the last century that the archæological value of fossils—their importance, I mean, as records of the history of the earth—was fully recognised; the first adequate investigation of the fossil remains of any large group of vertebrated animals is to be found in Cuvier's "Recherches sur les Ossemens Fossiles," completed in 1822; and, so modern is stratigraphical palæontology, that its founder, William Smith, lived to receive the just recognition of his services by the award of the first Wollaston Medal in 1831.

But, although palæontology is a comparatively youthful scientific speciality, the mass of materials with which it has to deal is already prodigious. In the last fifty years the number of known fossil remains

of invertebrated animals has been trebled or quadrupled. The work of interpretation of vertebrate fossils, the foundations of which were so solidly laid by Cuvier, was carried on, with wonderful vigour and success, by Agassiz, in Switzerland, by Von Meyer, in Germany, and last, but not least, by Owen in this country, while, in later years, a multitude of workers have laboured in the same field. In many groups of the animal kingdom the number of fossil forms already known is as great as that of the existing species. In some cases it is much greater; and there are entire orders of animals of the existence of which we should know nothing except for the evidence afforded by fossil remains. With all this it may be safely assumed that, at the present moment, we are not acquainted with a tithe of the fossils which will sooner or later be discovered. If we may judge by the profusion yielded within the last few years by the Tertiary formations of North America, there seems to be no limit to the multitude of Mammalian remains to be expected from that continent, and analogy leads us to expect similar riches in Eastern Asia whenever the Tertiary formations of that region are as carefully explored. Again, we have as yet almost everything to learn respecting the terrestrial population of the Mesozoic epoch—and it seems as if the Western Territories of the United States were about to prove as instructive in regard to this point as they have in respect of Tertiary life. My friend Prof. Marsh informs me that, within two years, remains of more than 160 distinct individuals of mammals, belonging to twenty species and nine genera, have been found in a space not larger than the floor of a good-sized room; while beds of the same age have yielded 300 reptiles, varying in size from a length of 60 feet or 80 feet to the dimensions of a rabbit.

The task which I have set myself to-night is to endeavour to lay before you, as briefly as possible, a sketch of the successive steps by which our present knowledge of the facts of palæontology and of those conclusions from them which are indisputable has been attained; and I beg leave to remind you, at the outset, that in attempting to sketch the progress of a branch of knowledge to which innumerable labours have contributed, my business is rather with generalisations than with details. It is my object to mark the epochs of palæontology, not to recount all the events of its history.

That which I just now called the fundamental problem of palæontology, the question which has to be settled before any other can be profitably discussed, is this,—What is the nature of fossils? Are they, as the healthy common sense of the ancient Greeks appears to have led them to assume without hesitation, the remains of animals

and plants? Or are they, as was so generally maintained in the fifteenth, sixteenth, and seventeenth centuries, mere figured stones, portions of mineral matter which have assumed the forms of leaves and shells and bones, just as those portions of mineral matter which we call crystals take on the form of regular geometrical solids? Or, again, are they, as others thought, the products of the germs of animals and of the seeds of plants which have lost their way, as it were, in the bowels of the earth, and have achieved only an imperfect and abortive development? It is easy to sneer at our ancestors for being disposed to reject the first in favour of one or other of the last two hypotheses; but it is much more profitable to try to discover why they, who were really not one whit less sensible persons than our excellent selves, should have been led to entertain views which strike us as absurd. The belief in what is erroneously called spontaneous generation—that is to say, in the development of living matter out of mineral matter, apart from the agency of pre-existing living matter, as an ordinary occurrence at the present day—which is still held by some of us, was universally accepted as an obvious truth by them. They could point to the arborescent forms assumed by hoar-frost and by sundry metallic minerals as evidence of the existence in nature of a "plastic force" competent to enable inorganic matter to assume the form of organised bodies. Then, as every one who is familiar with fossils knows, they present innumerable gradations, from shells and bones which exactly resemble the recent objects, to masses of mere stone which, however accurately they repeat the outward form of the organic body, have nothing else in common with it; and, thence, to mere traces and faint impressions in the continuous substance of the rock. What we now know to be the results of the chemical changes which take place in the course of fossilisation, by which mineral is substituted for organic substance, might, in the absence of such knowledge, be fairly interpreted as the expression of a process of development in the opposite direction—from the mineral to the organic. Moreover, in an age when it would have seemed the most absurd of paradoxes to suggest that the general level of the sea is constant, while that of the solid land fluctuates up and down through thousands of feet in a secular ground swell, it may well have appeared far less hazardous to conceive that fossils are sports of nature than to accept the necessary alternative, that all the inland regions and highlands, in the rocks of which marine shells had been found, had once been covered by the ocean. It is not so surprising, therefore, as it may at first seem, that although such men as Leonardo da Vinci and Bernard Palissy took just views of the nature of fossils

the opinion of the majority of their contemporaries set strongly the other way; nor even that error maintained itself long after the scientific grounds of the true interpretation of fossils had been stated, in a manner that left nothing to be desired, in the latter half of the seventeenth century. The person who rendered this good service to palæontology was Nicholas Steno, professor of anatomy in Florence, though a Dane by birth. Collectors of fossils at that day were familiar with certain bodies termed "glossopetræ," and speculation was rife as to their nature. In the first half of the seventeenth century, Fabio Colonna had tried to convince his colleagues of the famous Accademia dei Lincei that the glossopetræ were merely fossil sharks' teeth, but his arguments made no impression. Fifty years later Steno re-opened the question, and, by dissecting the head of a shark and pointing out the very exact correspondence of its teeth with the glossopetræ left no rational doubt as to the origin of the latter. Thus far, the work of Steno went little further than that of Colonna, but it fortunately occurred to him to think out the whole subject of the interpretation of fossils, and the result of his meditations was the publication, in 1669, of a little treatise with the very quaint title of "De Solido intra Solidum naturaliter contento." The general course of Steno's argument may be stated in a few words. Fossils are solid bodies which by some natural process have come to be contained within other solid bodies—namely, the rocks in which they are imbedded; and the fundamental problem of palæontology, stated generally, is this—"Given a body endowed with a certain shape and produced in accordance with natural laws, to find in that body itself the evidence of the place and manner of its production."[1] The only way of solving this problem is by the application of the axiom that "like effects imply like causes," or as Steno puts it, in reference to this particular case, that "bodies which are altogether similar have been produced in the same way."[2] Hence, since the glossopetræ are altogether similar to sharks' teeth, they must have been produced by shark-like fishes; and since many fossil shells correspond, down to the minutest details of structure, with the shells of existing marine or freshwater animals, they must have been produced by similar animals; and the like reasoning is applied by Steno to the fossil bones of vertebrated animals, whether aquatic or terrestrial. To the obvious objection that many fossils are not altogether similar to their living analogues

[1] "De Solido intra Solidum," p. 5.—"Dato corpore certâ figurâ prædito et juxta leges naturæ producto, in ipso corpore argumenta invenire locum et modum productionis detegentia."

[2] "Corpora sibi invicem omnino similia simili etiam modo producta sunt."

differing in substance while agreeing in form, or being mere hollows or impressions, the surfaces of which are figured in the same way as those of animal or vegetable organisms, Steno replies by pointing out the changes which take place in organic remains imbedded in the earth, and how their solid substance may be dissolved away entirely, or replaced by mineral matter, until nothing is left of the original but a cast, an impression, or a mere trace of its contours. The principles of investigation thus excellently stated and illustrated by Steno in 1669, are those which have, consciously or unconsciously, guided the researches of palæontologists ever since. Even that feat of palæontology which has so powerfully impressed the popular imagination, the reconstruction of an extinct animal from a tooth or a bone, is based upon the simplest imaginable application of the logic of Steno. A moment's consideration will show, in fact, that Steno's conclusion that the glossopetræ are sharks' teeth implies the reconstruction of an animal from its tooth. It is equivalent to the assertion that the animal of which the glossopetræ are relics had the form and organisation of a shark; that it had a skull, a vertebral column, and limbs similar to those which are characteristic of this group of fishes; that its heart, gills, and intestines presented the peculiarities which those of all sharks exhibit; nay, even that any hard parts which its integument contained were of a totally different character from the scales of ordinary fishes. These conclusions are as certain as any based upon probable reasonings can be. And they are so, simply because a very large experience justifies us in believing that teeth of this particular form and structure are invariably associated with the peculiar organisation of sharks, and are never found in connection with other organisms. Why this should be we are not at present in a position even to imagine; we must take the fact as an empirical law of animal morphology, the reason of which may possibly be one day found in the history of the evolution of the shark tribe, but for which it is hopeless to seek for an explanation in ordinary physiological reasonings. Every one practically acquainted with palæontology is aware that it is not every tooth nor every bone which enables us to form a judgment of the character of the animal to which it belonged, and that it is possible to possess many teeth, and even a large portion of the skeleton of an extinct animal, and yet be unable to reconstruct its skull or its limbs. It is only when the tooth or bone presents peculiarities which we know by previous experience to be characteristic of a certain group that we can safely predict that the fossil belonged to an animal of the same group. Any one who finds a cow's grinder may be perfectly sure that it belonged to an animal which had two

complete toes on each foot, and ruminated; any one who finds a horse's grinder may be as sure that it had one complete toe on each foot and did not ruminate; but, if ruminants and horses were extinct animals of which nothing but the grinders had ever been discovered, no amount of physiological reasoning could have enabled us to reconstruct either animal, still less to have divined the wide differences between the two. Cuvier, in the "Discours sur les Révolutions de la Surface du Globe," strangely credits himself, and has ever since been credited by others, with the invention of a new method of palæontological research. But if you will turn to the "Recherches sur les Ossemens Fossiles" and watch Cuvier, not speculating, but working, you will find that his method is neither more nor less than that of Steno. If he was able to make his famous prophecy from the jaw which lay upon the surface of a block of stone to the pelvis of the same animal which lay hidden in it, it was not because either he, or any one else, knew, or knows, why a certain form of jaw is, as a rule, constantly accompanied by the presence of marsupial bones—but simply because experience has shown that these two structures are co-ordinated.

The settlement of the nature of fossils led at once to the next advance of palæontology—viz., its application to the deciphering of the history of the earth. When it was admitted that fossils are remains of animals and plants, it followed that, in so far as they resemble terrestrial or freshwater animals and plants, they are evidences of the existence of land or fresh water, and in so far as they resemble marine organisms, they are evidences of the existence of the sea at the time at which they were parts of actually living animals and plants. Moreover, in the absence of evidence to the contrary, it must be admitted that the terrestrial or the marine organisms implied the existence of land or sea at the place in which they were found while they were yet living. In fact, such conclusions were immediately drawn by everybody, from the time of Xenophanes downwards, who believed that fossils were really organic remains. Steno discusses their value as evidence of repeated alteration of marine and terrestrial conditions upon the soil of Tuscany in a manner worthy of a modern geologist. The speculations of De Maillet in the beginning of the eighteenth century turn upon fossils, and Buffon follows him very closely in those two remarkable works, the "Théorie de la Terre" and the "Époques de la Nature," with which he commenced and ended his career as a naturalist.

The opening sentences of the "Époques de la Nature" show

us how fully Buffon recognised the analogy of geological with archæological inquiries. "As in civil history we consult deeds, seek for coins, or decipher antique inscriptions in order to determine the epochs of human revolutions and fix the date of moral events; so, in natural history, we must search the archives of the world, recover old monuments from the bowels of the earth, collect their fragmentary remains, and gather into one body of evidence all the signs of physical change which may enable us to look back upon the different ages of nature. It is our only means of fixing some points in the immensity of space and of setting a certain number of waymarks along the eternal path of time."

Buffon enumerates five classes of these monuments of the past history of the earth, and they are all facts of palæontology. In the first place, he says, shells and other marine productions are found all over the surface and in the interior of the dry land; and all calcareous rocks are made up of their remains. Secondly, a great many of these shells which are found in Europe are not now to be met with in the adjacent seas; and, in the slates and other deep-seated deposits, there are remains of fishes and of plants of which no species now exist in our latitudes, and which are either extinct or exist only in more northern climates. Thirdly, in Siberia and in other northern regions of Europe and of Asia, bones and teeth of elephants, rhinoceroses, and hippopotamuses occur in such numbers that these animals must once have lived and multiplied in those regions, although at the present day they are confined to southern climates. The deposits in which these remains are found are superficial, while those which contain shells and other marine remains lie much deeper. Fourthly, tusks and bones of elephants and hippopotamuses are found, not only in the northern regions of the old world, but also in those of the new world, although, at present, neither elephants nor hippopotamuses occur in America. Fifthly, in the middle of the continents, in regions most remote from the sea, we find an infinite number of shells, of which the most part belong to animals of those kinds which still exist in southern seas, but of which many others have no living analogues; so that these species appear to be lost, destroyed by some unknown cause. It is needless to inquire how far these statements are strictly accurate; they are sufficiently so to justify Buffon's conclusions that the dry land was once beneath the sea; that the formation of the fossiliferous rocks must have occupied a vastly greater lapse of time than that traditionally ascribed to the age of the earth; that fossil remains indicate different climatal conditions to have obtained in former times, and especially that the polar regions were once warmer;

that many species of animals and plants have become extinct; and that geological change has had something to do with geographical distribution.

But these propositions almost constitute the framework of palæontology. In order to complete it but one addition was needed, and that was made, in the last years of the eighteenth century, by William Smith, whose work comes so near our own times that many living men may have been personally acquainted with him. This modest land surveyor, whose business took him into many parts of England, profited by the peculiarly favourable conditions offered by the arrangement of our secondary strata to make a careful examination and comparison of their fossil contents at different points of the large area over which they extend. The result of his accurate and widely-extended observations was to establish the important truth that each stratum contained certain fossils which are peculiar to it; and that the order in which the strata, characterised by these fossils, are superimposed one upon the other is always the same. This most important generalisation was rapidly verified and extended to all parts of the world accessible to geologists; and, now, it rests upon such an immense mass of observations as to be one of the best established truths of natural science. To the geologist this discovery was of infinite importance, as it enabled him to identify rocks of the same relative age, however their continuity might be interrupted or their composition altered. But to the biologist it had a still deeper meaning, for it demonstrated that, throughout the prodigious duration of time registered by the fossiliferous rocks, the living population of the earth had undergone continual changes, not merely by the extinction of a certain number of the species which at first existed, but by the continual generation of new species, and the no less constant extinction of old ones.

Thus, the broad outlines of palæontology, in so far as it is the common property of both the geologist and the biologist, were marked out at the close of the last century. In tracing its subsequent progress I must confine myself to the province of biology, and, indeed, to the influence of palæontology upon zoological morphology. And I accept this limitation the more willingly as the no less important topic of the bearing of geology and of palæontology upon distribution has been luminously treated in the address of the President of the Geographical Section.

The succession of the species of animals and plants in time being established, the first question which the zoologist or the botanist had to ask himself was, What is the relation of these successive species

one to another? And it is a curious circumstance that the most important event in the history of palæontology which immediately succeeded William Smith's generalisation was a discovery which, could it have been rightly appreciated at the time, would have gone far towards suggesting the answer, which was in fact delayed for more than half a century. I refer to Cuvier's investigation of the Mammalian fossils yielded by the quarries in the older Tertiary rocks of Montmartre, among the chief results of which was the bringing to light of two genera of extinct hoofed quadrupeds, the *Anoplotherium* and the *Palæotherium*. The rich materials at Cuvier's disposition enabled him to obtain a full knowledge of the osteology and of the dentition of these two forms, and consequently to compare their structure critically with that of existing hoofed animals. The effect of this comparison was to prove that the *Anoplotherium*, though it presented many points of resemblance with the pigs on the one hand, and with the ruminants on the other, differed from both to such an extent that it could find a place in neither group. In fact, it held, in some respects, an intermediate position, tending to bridge over the interval between these two groups, which in the existing fauna are so distinct. In the same way, the *Palæotherium* tended to connect forms so different as the tapir, the rhinoceros, and the horse. Subsequent investigations have brought to light a variety of facts of the same order, the most curious and striking of which are those which prove the existence, in the mesozoic epoch, of a series of forms intermediate between birds and reptiles—two classes of vertebrate animals which at present appear to be more widely separated than any others. Yet the interval between them is completely filled, in the mesozoic fauna, by birds which have reptilian characters on the one side, and reptiles which have ornithic characters, on the other. So, again, while the group of fishes termed ganoids is at the present time so distinct from that of the dipnoi, or mudfishes, that they have been reckoned as distinct orders, the Devonian strata present us with forms of which it is impossible to say with certainty whether they are dipnoi or whether they are ganoids.

Agassiz's long and elaborate researches upon fossil fishes, published between 1833 and 1842, led him to suggest the existence of another kind of relation between ancient and modern forms of life. He observed that the oldest fishes presented many characters which recall the embryonic conditions of existing fishes; and that, not only among fishes, but in several groups of the invertebrata which have a long palæontological history, the latest forms are more modified, more specialised than the earlier. The fact that the dentition of the older

tertiary ungulate and carnivorous mammals is always complete, noticed by Prof. Owen, illustrated the same generalisation.

Another no less suggestive observation was made by Mr. Darwin, whose personal investigations during the voyage of the *Beagle* led him to remark upon the singular fact, that the fauna which immediately precedes that at present existing in any geographical province of distribution presents the same peculiarities as its successor. Thus, in South America and in Australia, the later tertiary or quaternary fossils show that the fauna which immediately preceded that of the present day was, in the one case, as much characterised by edentates and in the other by marsupials as it is now, although the species of the older are largely different from those of the newer fauna.

However clearly these indications might point in one direction, the question of the exact relation of the successive forms of animal and vegetable life could be satisfactorily settled only in one way—namely, by comparing, stage by stage, the series of forms presented by one and the same type throughout a long space of time. Within the last few years this has been done fully in the case of the horse-less completely in the case of the other principal types of the ungulata and of the carnivora, and all these investigations tend to one general result—namely, that in any given series the successive members of that series present a gradually increasing specialisation of structure. That is to say, if any such mammal at present existing has specially modified and reduced limbs or dentition and complicated brain, its predecessors in time show less and less modification and reduction in limbs and teeth, and a less highly developed brain. The labours of Gaudry, Marsh, and Cope furnish abundant illustrations of this law from the marvellous fossil wealth of Pikermi and the vast uninterrupted series of tertiary rocks in the territories of North America.

I will now sum up the results of this sketch of the rise and progress of palæontology. The whole fabric of palæontology is based upon two propositions: the first is, that fossils are the remains of animals and plants; and the second is, that the stratified rocks in which they are found are sedimentary deposits; and each of these propositions is founded upon the same axiom that like effects imply like causes. If there is any cause competent to produce a fossil stem, or shell, or bone, except a living being, then palæontology has no foundation; if the stratification of the rocks is not the effect of such causes as at present produce stratification, we have no means of judging of the duration of past time, or of the order in which the forms of life have succeeded one another. But, if these two propositions are granted,

there is no escape, as it appears to me, from three very important conclusions. The first is that living matter has existed upon the earth for a vast length of time, certainly for millions of years. The second is that, during this lapse of time, the forms of living matter have undergone repeated changes, the effect of which has been that the animal and vegetable population at any period of the earth's history contains some species which did not exist at some antecedent period, and others which ceased to exist at some subsequent period. The third is that in the case of many groups of mammals and some of reptiles, in which one type can be followed through a considerable extent of genealogical time, the series of different forms by which the type is represented at successive intervals of this time is exactly such as it would be if they had been produced by the gradual modification of the earliest form of the series. These are facts of the history of the earth guaranteed by as good evidence as any facts in civil history.

Hitherto I have kept carefully clear of all the hypotheses to which men have at various times endeavoured to fit the facts of palæontology, or by which they have endeavoured to connect as many of these facts as they happened to be acquainted with. I do not think it would be a profitable employment of our time to discuss conceptions which doubtless have had their justification and even their use, but which are now obviously incompatible with the well-ascertained truths of palæontology. At present these truths leave room for only two hypotheses. The first is that, in the course of the history of the earth, innumerable species of animals and plants have come into existence, independently of one another, innumerable times. This, of course, implies either that spontaneous generation on the most astounding scale, and of animals such as horses and elephants, has been going on, as a natural process, through all the time recorded by the fossiliferous rocks; or it necessitates the belief in innumerable acts of creation repeated innumerable times. The other hypothesis is, that the successive species of animals and plants have arisen, the later by the gradual modification of the earlier. This is the hypothesis of evolution; and the palæontological discoveries of the last decade are so completely in accordance with the requirements of this hypothesis that, if it had not existed, the palæontologist would have had to invent it.

I have always had a certain horror of presuming to set a limit upon the possibilities of things. Therefore I will not venture to say that it is impossible that the multitudinous species of animals and plants may have been produced one separately from the other by spontaneous generation, nor that it is impossible that they should

have been independently originated by an endless succession of miraculous creative acts. But I must confess that both these hypotheses strike me as so astoundingly improbable, so devoid of a shred of either scientific or traditional support, that even if there were no other evidence than that of palæontology in its favour, I should feel compelled to adopt the hypothesis of evolution. Happily, the future of palæontology is independent of all hypothetical considerations. Fifty years hence, whoever undertakes to record the progress of palæontology will note the present time as the epoch in which the law of succession of the forms of the higher animals was determined by the observation of palæontological facts. He will point out that, just as Steno and as Cuvier were enabled from their knowledge of the empirical laws of co-existence of the parts of animals to conclude from a part to the whole, so the knowledge of the law of succession of forms empowered their successors to conclude, from one or two terms of such a succession, to the whole series, and thus to divine the existence of forms of life, of which, perhaps, no trace remains, at epochs of inconceivable remoteness in the past.

XXX

A CONTRIBUTION TO THE PATHOLOGY OF THE EPIDEMIC KNOWN AS THE "SALMON DISEASE"

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(*Read March 2nd*, 1882.)

FOR some years, an epidemic disease, followed by a very large number of deaths, has been observed to prevail among the salmon of certain Scottish and British rivers, from the Tay,[1] on the north, as far as the Conway on the south.

The first obvious symptom of the malady is the appearance of one or more greyish patches upon the skin of parts of the body which are not covered with scales, such as the top and sides of the head, the adipose fin, and the soft skin at the bases of the other fins.

Such a patch, when it first attracts attention, may be as big as a sixpence. It is nearly circular, with a well defined margin and a somewhat raised softer centre, from which faint ridges radiate towards the circumference. It is important to observe that a single small patch of this kind may be seen on the skin of a fish which, in all other respects, is perfectly healthy, and when there is no indication that the skin has ever been bruised or abraded in the place occupied by the patch. The patch, once formed, rapidly increases in size and becomes confluent with any other patches which may have appeared in its neighbourhood. The marginal area, as it extends over the adjacent healthy skin, retains its characters; but the central part undergoes an important change. It takes on the consistency of wet paper, and can be lifted up in soft flakes, as if it were a slough, from the surface of the derma or true skin, which it covers. In fact, it is obvious that this papyraceous substance has taken the place of the epidermis, so that the sensitive and vascular true skin is deprived of its natural protection. As the patch spreads, the true skin beneath

[1] Within the last few days I have received specimens of diseased fish from the North Esk. (March 8.)

the central papyraceous slough ulcerates and an open bleeding sore is formed, which may extend down to the bone, while it passes outwards into burrowing sinuses.

When the disease has reached this stage it obviously causes great irritation. The fish dash about and rub themselves against stones, and thus, in all probability, aggravate the evils under which they suffer. One vast open sore may cover the top of the head from the snout to the nape, and may extend over the gill covers. The edges of the fins become ragged; and, sometimes, the skin which invests them is so completely frayed away that the fin-rays stand out separately.

Although the affection of the skin appears, usually, if not invariably, to commence in the scaleless parts of the body, it does not stop there, but gradually spreads over the whole of the back and sides of the fish, though I have not yet seen a specimen in which it covered the whole ventral surface. The disease extends into the mouth, especially affecting the delicate valvular membrane attached to the inner sides of the upper and the lower jaws. It is said to attack the gills, but there has been no sign of it on these organs in any fish which I have had the opportunity of examining.

Fish which succumb to the disease become weak and sluggish, seeking the shallows near the banks of the river, where they finally die.

The flesh of a salmon affected by this disease presents no difference in texture or colour from that of a healthy fish; and those who have made the experiment declare that the flavour is just as good in the former case as in the latter. So far as my observations have gone the viscera may be perfectly healthy in the most extensively diseased fish; and there is no abnormal appearance in the blood.

It is known that a disease similar to that described is occasionally prevalent among salmon in North America and in Siberia; and I do not see any ground for the supposition that it is a novelty in British rivers. But public attention was first directed to it in consequence of its ravages in the Solway district a few years ago; and, in 1879, a Commission was appointed by Sir Richard Cross, then Home Secretary, to inquire into the subject.

The evidence taken by the Commissioners[1] leaves no room for

[1] "Report on the Disease which has recently prevailed among the Salmon in the Tweed, Eden, and other Rivers in England and Scotland." By Messrs. Buckland, Walpole, and Young, 1880.

See also the three valuable communications to the "Proceedings of the Royal Society of Edinburgh," made by the late Mr. A. B. Stirling in 1878-79.

doubt that the malady is to be assigned to the large and constantly increasing class of diseases which are caused by parasitic organisms. It is a contagious and infectious disease of the same order as ringworm in the human subject, muscardine among silkworms, or the potato disease among plants; and, like them, is the work of a minute fungus. In fact, the *Saprolegnia* which is the cause of the salmon disease is an organism in all respects very closely allied to the *Peronospora*, which is the cause of the potato disease.

It is a very curious circumstance, however, that while the *Peronosporæ* are always parasites—that is to say, depend altogether upon living plants for their support—the *Saprolegniæ* are essentially saprophytes; that is to say, they ordinarily derive their nourishment from dead animal and vegetable matters, and are only occasionally parasites upon living organisms. In this respect they resemble the *Bacteria*, if the results of recent researches, which tend to show that pathogenic bacteria are mere modifications of saprogenic forms, are to be accepted.

As I have said, I do not think that the evidence laid before the Commission of 1879 can leave any doubt as to the causation of the salmon disease on the minds of those who are acquainted with the history of the analogous diseases in other animals and in plants. Nevertheless, this evidence, valuable as it is, suggests more questions than it answers, and in November, 1881, hearing that the disease had broken out in the Conway, I addressed myself to the attempt to answer some of these.

It was already known that when the papyraceous slough-like substance which coats the skin of a diseased salmon is subjected to microscopic examination, it is found to be a *mycelium*, or fungus-turf composed of a felt-work of fine tubular filaments or *hyphæ*, many of which are terminated by elongated oval enlargements, or *zoosporangia*. Within these the protoplasm breaks up into numerous spheroidal particles, each less than $\frac{1}{2000}$ of an inch in diameter. These, the *zoospores*, are set free through an opening formed at the apex of the zoosporangium, and become actively or passively dispersed through the surrounding water. Herein lies the source of the contagiousness or infectiousness of the disease. For any one of these zoospores, reaching a part of the healthy skin of the same or of another salmon, germinates and soon gives rise to a mycelium similar to that from which it started.

But I could find no satisfactory information as to the manner in which the fungus enters the skin, how far it penetrates, the exact nature of the mischief which it does, or what ultimately becomes of

it; nor was the identity of the pathogenic *Saprolegnia* of the salmon with that of any known form of saprogenic *Saprolegnia* demonstrated. It appeared to me, however, to be useless to attempt to deal with the disease until some of these important elements of the question were determined.

To this end, in the first place, I made a careful examination of the minute structure of both the healthy and diseased skin, properly hardened and cut into thin sections; and, in the second place, I tried some experiments on the transplantation of the *Saprolegnia* of the living salmon to dead animal bodies. Perhaps it will conduce to intelligibility if I narrate the results of the latter observations first.

The body of a recently killed common house-fly was gently rubbed two or three times over the surface of a patch of the diseased skin of a salmon and was then placed in a vessel of water, on the surface of which it floated, in consequence of the large quantity of air which a fly's body contains. In the course of forty-eight hours, or thereabouts, innumerable white cottony filaments made their appearance, set close side by side, and radiated from the body of the fly in all directions. As these filaments had approximately the same length, the fly's body thus became inclosed in a thick white spheroidal shroud, having a diameter of as much as half an inch. As the filaments are specifically heavier than water, they gradually overcome the buoyancy of the air contained in the tracheæ of the fly, and the whole mass sinks to the bottom of the vessel. The filaments are very short when they are first discernible, and usually make their appearance where the integument of the fly is softest, as between the head and thorax, upon the proboscis, and between the rings of the abdomen. These filaments, in their size, their structure, and the manner in which they give rise to zoosporangia and zoospores are precisely similar to the hyphæ of the salmon fungus; and the characters of the one, as of the other, prove that the fungus is a *Saprolegnia* and not an *Achlya*. Moreover, it is easy to obtain evidence that the body of the fly has become infected by spores swept off by its surface when it was rubbed over the diseased salmon skin. These spores have in fact germinated, and their hyphæ have perforated the cuticle of the fly, notwithstanding its comparative density, and have then ramified outwards and inwards, growing at the expense of the nourishment supplied by the tissues of the fly.

This experiment, which has been repeated with all needful checks, proves that the pathogenic *Saprolegnia* of the living salmon may become an ordinary saprogenic *Saprolegnia*; and, *per contra*, that the latter may give rise to the former; and they lead to the important

practical conclusion that the cause of salmon disease may exist in all waters in which dead insects, infested with *Saprolegniæ*, are met with; that is to say, probably in all the fresh waters of these islands, at one time or another.

On the other hand, *Saprolegnia* has never been observed on decaying bodies in salt water, and there is every reason to believe that, as a saprophyte, it is confined to fresh waters.[1]

Thus it becomes, to say the least, a highly probable conclusion that we must look for the origin of the disease to the *Saprolegniæ* which infest dead organic bodies in our fresh waters. Neither pollution, drought, nor overstocking will produce the disease if the *Saprolegnia* is absent. The most these conditions can do is to favour the development or the diffusion of the *materies morbi* where the *Saprolegnia* already exists.

Having infected dead flies with the salmon *Saprolegnia*, once from Conway and once from Tweed fish,[2] I was enabled to propagate it from these flies to other flies, and, in this manner, to set up a sort of garden of *Saprolegniæ*. And having got thus far, I fancied it would be an easy task to determine the exact species of the *Saprolegnia* with which I was dealing, from the abundant data furnished by the works of Pringsheim, De Bary, and others, who have so fully studied these plants when cultivated on the same materials. For this purpose, it was necessary to obtain the oosporangia; and, in ordinary course, these should have made their appearance on my *Saprolegniæ* in five or six days. Unfortunately, in the course of cultivations continued over two months, nothing of the kind has taken place. Zoosporangia have abounded in the ordinary form and also in that known as "dictyosporangium," but, in no instance, have any oosporangia appeared. After a few days of vigorous growth, the zoosporangia become scanty, and the fungus takes on a torulose form, segments of the hyphæ becoming swollen and then detached as independent "gemmæ," which may germinate. Sometimes the gemmæ are spheroidal and terminal, and closely simulate oosporangia.

Although, therefore, I have very little doubt that the *Saprolegnia* of the salmon is one of the forms of the "*S. ferax* group" of Pringsheim and De Bary, I have, at present, no proof of the fact.

Another very curious and unexpected peculiarity of the salmon *Saprolegnia*, both on the fish and when transmitted to flies, so far as my observations have hitherto gone, is that locomotive ciliated

[1] So far as I know, there is only one case on record of the appearance of a fungus on a fish in salt water, and in this case it is not certain that the fungus was a *Saprolegnia*.

[2] And since this paper was read once more from the North Esk fish. (March 8, 1882.)

zoospores do not occur. I once saw one which exhibited a very slight motion for a few minutes after it left the zoosporangium; but although thousands must have passed under my notice, with the exception to which I have referred, they have always been perfectly quiescent and not unfrequently in different stages of germination. Whether the season of the year, or the conditions under which my saprolegnised flies were placed, have anything to do with the non-appearance of oosporangia and of locomotive zoospores in them I cannot say. But it is certain that the *Saprolegnia ferax* which commonly appears upon dead flies and other insects normally develops both oosporangia and locomotive zoospores in abundance.

From such notices by other observers as I can gather, oosporangia appear to be of very rare occurrence in the *Saprolegnia* of the salmon itself. Mr. Stirling mentions that he has met with them only four times. With respect to locomotive zoospores, I can find no positive evidence that they have been regularly, or even frequently observed in the salmon *Saprolegnia*. But these points require careful investigation on freshly taken diseased fish.

Whether the zoospores are actively locomotive or not, they are quite free when they emerge from the zoosporangia; and, from their extreme minuteness, they must be readily carried away and diffused through the surrounding water. Hence, a salmon entering a stream inhabited by the *Saprolegnia* will be exposed to the chance of coming into contact with *Saprolegnia* spores; and the probability of infection, other things being alike, will be in proportion to the quantity of the growing *Saprolegnia*, and the vigour with which the process of spore-formation is carried on. At a very moderate estimate, a single fly may bear 1,000 fruiting hyphæ; and if each sporangium contains twenty zoospores, and runs through the whole course of its development in twelve hours, the result will be the production of 40,000 zoospores in a day, which is more than enough to furnish one zoospore to the cubic inch of twenty cubic feet of water. Even if we halve this rate of production, it is easy to see that the *Saprolegnia* on a single fly might furnish spores enough to render such a small shallow stream as salmon often ascend for spawning purposes, dangerous for several days. But a large fully diseased salmon may have as much as two square feet of its skin thickly covered with *Saprolegnia*. If we allow only 1,000 fruiting hyphæ for every square inch, we shall have 288,000 for the whole surface, which, at the same rate as before, gives over 10,000,000 spores for a day's production, or enough to provide a spore to every cubic foot of a mass of water 100 feet wide and 5 feet deep and four

miles long. Forty such diseased salmon might furnish one spore to the gallon for all the water of the Thames (380,000,000 gallons per diem) which flows over Teddington Weir. But two thousand diseased salmon have been taken out of a single comparatively insignificant river in the course of a season.

It will be understood that the above numerical estimate of the productivity of *Saprolegnia*, has been adopted merely for the sake of illustration; that I do not intend to suggest that the zoospores are evenly distributed through the water into which they are discharged by the zoosporangia; and that allowance must be made for the very short life of those zoospores which do not speedily reach an appropriate nidus. Nevertheless, the conclusion remains arithmetically certain that every diseased salmon adds immensely to the chances of infection of those which are not diseased; and thus, the policy of extirpating every diseased fish as soon as possible, has ample justification. But, in practice, the attempt to stamp out the disease in this fashion would be so costly that it may be a question whether it is not better to put up with the loss caused by the malady.

There are many practical difficulties in the way of directly observing the manner in which the zoospores effect their entrance into the skin of the fish; but, on comparing the structure of the healthy integument with that of the diseased patches, the manner of the operation can readily be divined. The skin of the head of a salmon, for example, presents a thin superficial cellular epidermis covering the deep fibrous and vascular derma. The epidermic cells are distinguishable, as in fishes in general, into a deep, a middle, and a superficial layer. In the first, the cells are vertically elongated, in the second more rounded and polygonal, in the third flattened. Many of the cells of the middle layer are of the nature of "mucous cells." They enlarge and become filled with a mucous secretion; and, rising to the surface, burst and discharge their contents, which give rise to the mucous fluid with which the fish's body is covered. The openings of these "mucous cells" remain patent for some time and are to be seen in thin vertical sections. The hyphæ of the spores which attach themselves to the fish may enter by these openings, but even if they do not, the flattened superficial cells certainly offer no greater resistance than does the tough cuticle of a fly. However this may be, sections of young patches of diseased skin show that the hyphæ of the fungus not only traverse the epidermis, but bore through the superficial layer of the derma for a distance, in some cases, of as much as one-tenth of an inch. Each hypha thus comes to have a stem part, which lies in the epidermis, and a root-part,

which lies in the derma. Each of these elongates and branches out. The free ends of the stem-hyphæ rise above the surface of the epidermis and become converted into zoosporangia, more or fewer of the spores of which attach themselves to the surrounding epidermis and repeat the process of penetration. Thus the epidermis and the derma become traversed by numerous hyphæ set close side by side. But, at the same time, these hyphæ send off lateral branches which spread radially, forcing asunder the middle and deeper layers of the epidermic cells, and giving rise to the radiating ridges which are visible to the naked eye in the peripheral part of the patch. The force of the growth of the hyphæ which traverse the epidermis, is made obvious by the curious manner in which, when the central tract of a patch is teased out, the distorted epidermic cells are seen adhering to it, as if they were spitted upon it.

In the derma, the root-hyphæ branch out, pierce the bundles of connective tissue, and usually end in curiously distorted extremities.

The effect of the growth of the stem-hyphæ is to destroy the epidermis altogether. Its place is taken by a thick, felted, mycelium, which entangles the minute particles of sand which are suspended in the water, and thus no doubt constitutes a very irritating application to the sensitive surface of the true skin.

In the true skin, the tracks of the root-hyphæ are not accompanied by any obvious signs of inflammation, but the hyphæ are so close set, that they cannot fail to interfere with the nutrition of the part, and thus bring about necrosis and sloughing. Such sloughing in fact gradually takes place, small vessels give way and bleed, and the burrowing sore, which is characteristic of the advanced stages of the disease, is produced.

The skin of the head may thus be eaten away down to the bone and gristle of the skull, but I have not observed the fungus to enter these. On the scaly part of the skin, the fungus burrows in the superficial and in the deep layer of the pouches of the scales, but I have not observed the scales themselves to be perforated.

When I found that the fungus penetrated the true skin, and thus gained access to the lymphatic spaces and blood-vessels, it became a matter of great interest to ascertain whether the hyphæ might not break up into toruloid segments (as in the case of the *Empusa muscæ*), and thus give rise to general septic poisoning, or fungoid metastasis. However, I have never been able to find any indication of the occurrence of such a process.

But a very important practical question arises out of the discovery that the fungus penetrates into the derma. There is much reason to

believe, that if a diseased salmon returns to salt water, all the fungus which is reached by the saline fluid is killed, and the destroyed epidermis is repaired. But the sea water has no access to the hyphæ which have burrowed into the true skin; and hence it must be admitted to be possible, that, in a salmon which has become to all appearance healed in the sea, and which looks perfectly healthy when it ascends a river, the remains of the fungus in the derma may break out from within, and the fish become diseased without any fresh infection. It has not infrequently been observed, that salmon in their upward course became diseased at a surprisingly short distance from the sea, and it is possible that the explanation of the fact is to be sought in the revival of dormant *Saprolegnia*, rather than in new infection. It is to be hoped, that experiments, now being carried on at Berwick, will throw some light on this point, as well as upon the asserted efficacy of sea water in destroying the fungus which it reaches.

These are the chief results of this season's observations on the salmon disease. Incomplete as they are, they appear to me to justify the following conclusions:—

1. That the *Saprolegnia* attacks the healthy living salmon exactly in the same way as it attacks the dead insect, and that it is the sole cause of the disease, whatever circumstances may, in a secondary manner, assist its operations.

2. That death may result without any other organ than the skin being attacked, and that, under these circumstances, it is the consequence partly of the exhaustion of nervous energy by the incessant irritation of the felted mycelium with its charge of fine sand, and partly of the drain of nutriment directly and indirectly caused by the fungus.

3. That the penetration of the hyphæ of the *Saprolegnia* into the derma renders it at least possible that the disease may break out in a fresh-run salmon without re-infection.

4. That the cause of the disease, the *Saprolegnia*, may flourish in any fresh water, in the absence of salmon, as a saprophyte upon dead insects and other animals.

5. That the chances of infection for a healthy fish entering a river are prodigiously increased by the existence of diseased fish in that river, inasmuch as the bulk of *Saprolegnia* on a few diseased fish vastly exceeds that which would exist without them.

6. That, as in the case of the potato disease, the careful extirpation of every diseased individual is the treatment theoretically indicated; though, in practice, it may not be worth while to adopt that treatment.

XXXI

ON THE RESPIRATORY ORGANS OF *APTERYX*

Proceedings of the Scientific Meetings of the Zoological Society of London for the Year 1882, *pp.* 560–569. (*Read June 20th*, 1882.)

I AM not aware that the structure of the respiratory organs of *Apteryx* has been investigated since the publication of Professor Owen's Memoirs on the Anatomy of the Southern Apteryx, in the second and third volumes of the 'Transactions' of this Society. Professor Owen gives a detailed description of a structure which he terms the diaphragm, and compares it with that organ in mammals; the account of the anatomy of the lungs and of the air-sacs, on the other hand, is less full. The important fact that no air-sac extends into the abdomen is noted; but only four air-sacs on each side are mentioned, and no attempt is made to identify these with the air-sacs of other birds.

The question whether *Apteryx* presents any real approximation to mammals in the structure of its breathing apparatus is of considerable interest, from its bearing upon the general problem of the affinities of birds to other groups of vertebrated animals. Having recently examined a specimen of *Apteryx* (which, although it had been many years in spirit, was still in a very fair state of preservation) with reference to this point, I have come to the conclusion that its respiratory organs differ in no essential respect from those of other birds—though they exhibit those peculiarities which are peculiar to and characteristic of the class Aves in a less developed condition than that which obtains in all those Carinatæ and Ratitæ which have been carefully studied.

The admirable monograph by Sappey,[1] chiefly based on the study of the respiratory organs of the Duck, contains the most complete and

[1] Recherches sur l'Appareil respiratoire des Oiseaux: 1847.

accurate account extant of the general disposition of these organs in their highest condition of development. Rainey[1] supplemented this by the important discovery of the existence of intercapillary air-passages; and, more recently, Campana[2] has contributed a very elaborate study of the respiratory organs of the Common Fowl. It is not difficult to verify the chief statements of these anatomists. Nevertheless it is anything but easy to find a succinct and precise account of the facts; and the terminology at present employed appears to me to be for the most part cumbrous and inappropriate. I make no apology, therefore, for endeavouring to amend this state of matters.

The lungs of birds lie, one on each side of the vertebral column, between the first thoracic rib in front and the anterior end of the kidney behind. On the dorsal aspect they rise, on the sides of the vertebræ, as high as the tubercular transverse processes of the ribs. On the ventral aspect they descend to a variable distance towards the ends of the vertebral ribs. The lowest point of the ventral margin lies on one of these ribs, not far from its articulation with the sternal rib; and the hinder part of this margin, or the ***posterior ventral margin***, slopes upwards and backwards, while the ***anterior ventral margin*** is inclined upwards and forwards from this point, which may be called the *ventral angle* of the lung. The whole ventral margin of the lung is very thin; its dorsal margin, on the other hand, is thick and rounded off into the outer or lateral face of the lung, which is convex from above downwards. The dorsal margin and the lateral face are closely applied to the parietes; and the former presents deep notches, into which the necks and dorsal portions of the bodies of the ribs are received.

The mesial face of the lung is divisible into three facets:—a *superior*, which is closely applied to the lateral faces of the vertebræ and to a fibrous lamella, the *median vertical septum*, which proceeds from the ventral faces of the vertebræ in the middle line; and an *anterior inferior* and a *posterior inferior* facet, which occupy that slightly concave face of the lung which is turned towards the thoracic cavity. These last facets are divided by a ridge or elevation of the surface of the lung, which ascends from the ventral angle to the insertion of the bronchus. This is always situated at some considerable distance from the anterior end of the lung.

The anterior inferior and posterior inferior facets of the lung are closely invested by a thin fibrous membrane, which may be termed

[1] "On the minute Structure of the Lung of the Bird," Medico-Chirurgical Transactions, xxxii. 1849.

[2] Les Lois de l'Evolution animale.—La Respiration des Oiseaux: 1875.

the *pulmonary aponeurosis* ("diaphragme pulmonaire," Sappey; "diaphragmite antérieur," Milne-Edwards). The mesial edge of this is continuous with the median vertical septum; the lateral edge is inserted into the parietes of the thorax immediately beyond the ventral edge of the lung. Around the pneumatic apertures, or *ostia*, the pulmonary aponeurosis is closely adherent to their margins; it is, in fact, perforated by them.

Broad flat bands of striated muscle (the *costo-pulmonary muscles*) take their origin from the vertebral ribs,[1] at some distance below the attachment of the pulmonary aponeurosis, and, proceeding obliquely dorsad and forwards, spread out and are inserted into that part of the aponeurosis which covers the posterior inferior facet. They are supplied with branches of the intercostal nerves. This pulmonary aponeurosis with its muscles is one of the two structures which have been compared to the mammalian diaphragm.

The second so-called "diaphragm" ("diaphragme thoraco-abdominal," Sappey; "diaphragmite thoraco-abdominal," Milne-Edwards) is a more or less aponeurotic fibrous membrane, continuous with the ventral edge of the median dorsal septum and suspended by it, like the roof of a tent, across the thoraco-abdominal cavity. In the middle line, this *oblique septum* slopes downwards and forwards to the dorsal and anterior face of the pericardium, with which its fibres become firmly connected on their way to their attachment to the sternum. From the median line, the two halves of the oblique septum slope laterally and ventrally until they attach themselves to the parietes of the abdomen behind, to those of the thorax more anteriorly, and to the margins of the sternum in front, at a considerable distance from the attachment of the pulmonary aponeurosis. It follows that a wide interspace is left, on each side, between the pulmonary aponeurosis, dorsally and laterally, the dorsal median septum in the middle line, the oblique septum ventrally and below, and the parietes of the body laterally; and, as the mesial attachments of the pulmonary aponeurosis and of the oblique septum are very much closer together than their outer attachments, the whole cavity has somewhat the form of a wedge with the narrow edge towards the middle line. This *subpulmonary chamber* is divided into four *loculi* by three *dissepiments*, which pass transversely from the lateral face of the oblique septum to the mesial face of the pulmonary aponeurosis. Each loculus lodges one of four *postbronchial* saccular diverticula of the wall of the lung, constituting the proper air-sacs, which thus fill

[1] In many birds there are additional "*sterno-pulmonary*" *muscles*, which proceed from the antero-lateral part of the sternum to the aponeurosis covering the anterior inferior facet.

up the subpulmonary chamber, between the insertion of the bronchus and its posterior extremity. Another air-sac lies in front of the insertion of the bronchus, on the mesial side of the anterior extremity of the lung.

Thus, on each side, there are five air-sacs, the lateral and superior face of each of which abuts against a particular region of the lung. The most anterior is that just mentioned, which may be called *præbronchial* (" réservoir cervical," Sappey), as the bronchus lies between it and the next, or *subbronchial* (" interclavicular," Sappey). The dissepiment which separates the loculus of this sac from the next is attached mesially along the oblique elevation which runs from the insertion of the bronchus to the ventral margin of the lung. The following dissepiment is attached dorsally, near the origin of the cœliac artery from the aorta, which lies in the median dorsal septum, and thence to the pulmonary aponeurosis, along a line which is inclined more or less obliquely backwards, to the posterior ventral margin. It separates two loculi, which lodge the *anterior* and the *posterior intermediate* air-sacs (" réservoir diaphragmatique antérieur et postérieur," Sappey). The third dissepiment, still more inclined, divides the loculus of the posterior intermediate air-sac from that of the *posterior* air-sac (" réservoir abdominal," Sappey).

Thus, that part of the thoraco-abdominal cavity which lies dorsad and anterior to the oblique septum lodges no other viscera than the lungs and the air-sacs, and may therefore be distinguished, as the *respiratory cavity*, from the *cardio-abdominal cavity*, which contains the heart and the rest of the viscera, and lies below and behind the oblique septum. The respiratory cavity is further divided into two lateral chambers by the median dorsal septum ; and each of these chambers is subdivided by the pulmonary aponeurosis into two stories, of which the upper is occupied by the lung, and the lower by the loculi with their contained air-sacs.

The dorsal aorta traverses the median dorsal septum from before backwards, giving off, from its ventral aspect, the cœliac and the mesenteric arteries, which thus appear in the middle line of the oblique septum when this is viewed from below and behind. The vena cava inferior enters the pericardium just behind the attachment of the oblique septum to it.

Immediately after the bronchus has entered the lung, it enlarges somewhat to form a dilatation, which has been termed the *vestibule.* A trunk which continues the direction of the bronchus through the centre of the parenchyma of the lung backwards, leaves the posterior end of the vestibule, and ends at the superior end of the posterior

ventral margin in the *posterior ostium*, by which it opens into the posterior air-sac. This trunk may be termed the *mesobronchium*, by way of distinction from certain others which have a superficial position on either the lateral or the mesial face of the lung; and which may be distinguished, respectively, as *ecto-* and *ento-bronchia*.

Toward the middle of its course the mesobronchium gives off a wide branch, which passes backwards and downwards to the posterior ventral edge of the lung, and opens there by a very wide *posterior intermediate ostium* into the corresponding air-sac.

The *entobronchia* ("bronches diaphragmatiques," Sappey) are four in number. They take their origin in wide openings of the dorsal wall of the vestibule. The *fourth* is hindermost, runs almost directly backwards to the posterior end of the lung, and ends there cæcally. Branches are given off only from its ventral wall.

The *third* entobronchium runs parallel with this, giving off a number of close-set branches from its dorsal side, which are distributed over the superior facet. Close to the entrance of the bronchus, this presents the large *anterior intermediate ostium* for the corresponding air-sac.

The *secona* entobronchium passes directly dorsad, and ramifies over the middle of the superior facet. A wide branch descends to the *subbronchial ostium*.

The *first* entobronchium curves sharply round the entrance of the bronchus, and from its anterior or convex wall gives off a number of branches to the anterior part of the superior facet and to the anterior inferior facet. One of these branches passes directly forwards, and opens by the *præbronchial ostium* into the præbronchial air-sac; while the inferior end of the trunk opens below the bronchus, into the subbronchial ostium, and, in that way, communicates with the subbronchial air-sac.

Thus the mesobronchium and the first entobronchium are each connected with two air-sacs—the former with the posterior two, and the latter with the anterior two; while the middle air-sac (anterior intermediate) communicates with the third entobronchium so close to the vestibule that it might almost be said to open into the latter.

Behind the vestibule, the mesobronchium gives off successively several (usually six or seven) branches, which are directed laterally and dorsally towards the lateral or costal face of the lung. These are the *ectobronchia* ("bronches costales," Sappey).

Those parts of the walls of the various bronchia and their ramifications, which are in relation with the pulmonary parenchyma, are perforated by minute rounded apertures. These lead into canals

which are directed, at first, more or less at right angles to the surfaces of the bronchia upon which they open, and pass, side by side, sometimes anastomosing with one another, to some other bronchium than that from which they start. They may be termed ***parabronchia*** ("canaux tertiaires," Cuvier; "bronchial tubes," Rainey; "Lungenpfeifen" of the Germans). The lumina of these canals are interrupted at pretty regular intervals by transverse circular folds which contain unstriped muscular fibres. The interspaces between these folds are more or less subdivided by oblique or longitudinal folds of a similar nature into *fossæ*; and the walls of these fossæ present smaller depressions or *fossulæ*, which directly, or indirectly, open into the ***intercapillary air-passages***. These last occupy the meshes of the capillary network into which the pulmonary vessels resolve themselves.

This description (with possibly some variation in the number of the ostia and air-sacs) applies to the respiratory apparatus of every known bird, and to that of no other animal; but it also applies, almost word for word, to *Apteryx*. Hence there can be no doubt that the respiratory organs of this bird are thoroughly and typically ornithic, and that they present not the slightest approximation to those of the Mammalia.

If the organs of respiration of *Apteryx* are compared with those of a carinate bird of similar size and form of trunk, such as a Duck, the resemblances and differences between the two can be easily traced.

1. The Duck's lungs are considerably larger both absolutely and relatively.

2. The anterior ventral margin in the Duck is longer than the posterior. The reverse obtains in *Apteryx*.

3. The pulmonary aponeurosis of the Duck is very delicate; in *Apteryx* it is strong and thick.

4. The median vertical septum in the Duck is much deeper, and anteriorly it is supported by the long hypapophyses of the anterior thoracic vertebræ. At the same time it is far less strongly fibrous than the corresponding structure in *Apteryx*. The mesial attachment of the pulmonary aponeurosis is to the ventral edge of the septum, close to that of the oblique septum, in the Duck; while in *Apteryx* the two are separated by a considerable interval, throughout which the thin and membranous part of the dorsal median septum divides the mesial ends of the intermediate and posterior loculi from one another.

In the Duck, the median dorsal septum lies throughout between

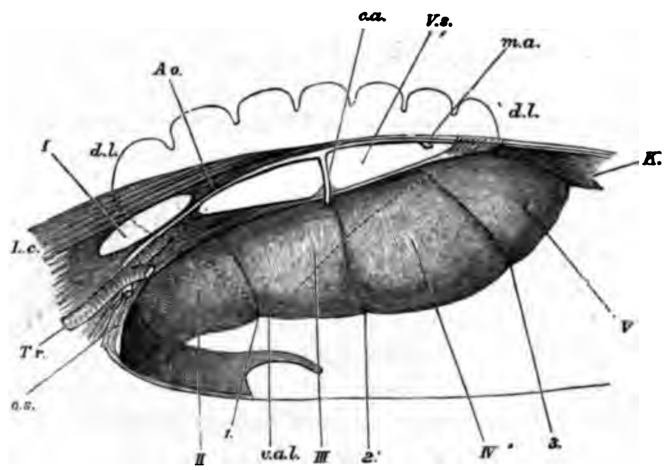


FIG. 1.

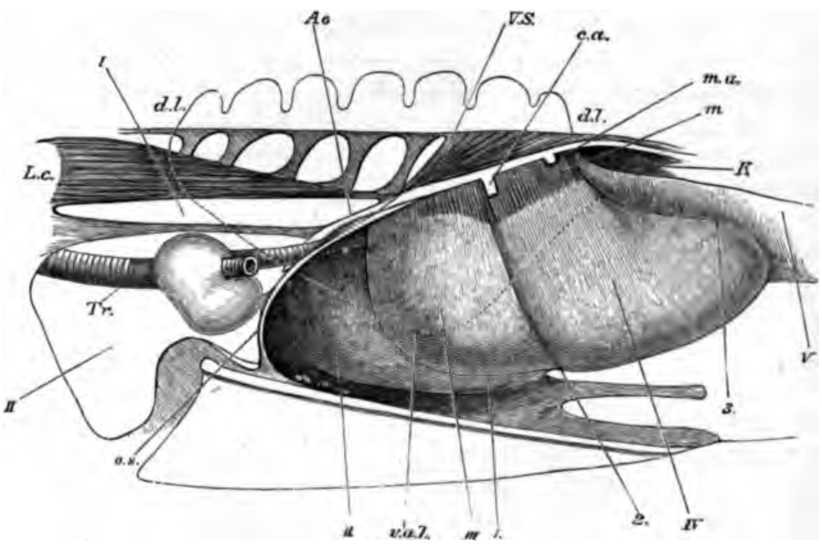


FIG. 2.

FIG. 1. Respiratory organs of *Apteryx*; and FIG. 2, of a Duck having the trunk of nearly the same dimensions. In each the vertebral column and the left wall of the thoracic and abdominal cavities are supposed to be removed; while the median vertical septum, the right half of the oblique septum, and the air-sacs of the right side are left. The contour of the right lung is indicated.

d. l, dorsal margin of the lung; *v. a. l*, ventral angle of the lung; I, præbronchial, II, infrabronchial, III, anterior intermediate, IV, posterior intermediate, V, posterior air-sac; 1, 2, 3, dissepiments.

L. c, *longus colli*; *V. s*, vertical median septum; *o. s*, oblique septum; *Tr*, trachea; *Ao*, aorta; *c. a*, cœliac artery; *m. a*, mesenteric artery; *K*, kidney. *m*, smooth muscular fibres in the oblique septum of the Duck.

the superior facets of the internal faces of the two lungs. In other words, this superior facet is much deeper in the Duck than in *Apteryx*.

5. The oblique septum is extremely thin and weak in the Duck; while in *Apteryx* it is a very strong aponeurotic membrane, with interlacing fibres diverging from two tendons attached to the under face of the posterior thoracic vertebræ. In the Duck it contains, on each side, a layer of unstriped muscular fibres. I have not been able to make out any such fibres in *Apteryx*.

6. The most remarkable difference, however, lies in the development of the air-sacs in the two birds.

In *Apteryx*, as in the Duck, the attachment of the dorsal end of the dissepiment between the intermediate loculi corresponds with the exit of the cœliac artery from the dorsal median septum; and the relation of the air-sacs in front of and behind this dissepiment to the bronchia which open into them is such, that there can be no question of their homology with the *anterior* and the *posterior intermediate* air-sacs in the Duck, notwithstanding the vastly greater size of the latter. Hence the air-sac in front of the anterior intermediate in *Apteryx* must be the homologue of the subbronchial in the Duck; and the position of this sac and its relation to the subbronchial ostium leave no doubt that such is the case.

But while, in *Apteryx*, the subbronchial air-sac does not extend beyond the front margin of the sternum, and is floored by that part of the oblique septum which lies at the sides of the fore part of the pericardium and is attached to the front edges of the sternum, in the Duck only a small part of the sac is thus related to the oblique septum, and even this extends much further backwards and more towards the median line than in *Apteryx*. In front, each of these sacs has enlarged forwards to the space between the furcula and the sternum, and there has opened into its fellow in the middle line. Thus the two subbronchial air-sacs are fused into one great air-chamber, and their mesial walls are so closely applied to the trachea and great vessels as to invest them like a serous coat. Moreover the common sac sends prolongations into the axillæ and elsewhere, and communicates with the pneumatic cavities of the adjacent bones. A similar modification has taken place in the posterior air-sacs of the Duck, but has been carried to a still greater extent. In *Apteryx* the whole of this sac is enclosed between the oblique septum and the pulmonary aponeurosis, the dissepiment between its loculus and that of the posterior intermediate sac being situated almost midway between the second dissepiment and the posterior extremity of the

pneumatic chamber. In the Duck, on the contrary, the dorsal end of this dissepiment is attached close to the posterior extremity of the lung, and thence slopes very obliquely backwards. The capacity of the posterior intermediate air-sac thus becomes greatly increased. But, as the capacity of the posterior air-sac is also vastly greater than in *Apteryx*, its posterior wall has been, apparently, driven out, like a hernial sac, between the peritoneum and the parietes, and projects into the abdominal cavity. It would be incorrect, therefore, to say that the abdominal air-sac is absent in *Apteryx*: it is just as much present as in any other bird; but its small size and the small relative development of the posterior intermediate sac permit it to occupy a different position.

7. The first or præbronchial air-sac has hitherto been overlooked in *Apteryx*. It is of a long ovate or spindle-shape, 21 millim. long by 8 millim. wide in the middle, and lies between the *longus colli* with the vertebral column above, and the œsophagus and bronchus below. Laterally, it is bounded by so much of the anterior facet of the lung as lies above the level of the bronchus. Mesially, it is widely separated from its fellow by the fibrous tissue continued from the anterior end of the median vertical septum on to the œsophagus, bronchi, and aorta.

The præbronchial air-sac in the Duck is fully three times as long, and sends off prolongations to the vertebral column, which have been described by Sappey.

8. The vestibule, mesobronchium, and entobronchia of *Apteryx* present no important differences from those of the Duck, except that the branches of the entobronchia are less numerous.

The ectobronchia, on the other hand, are much smaller, and only the most anterior reaches the lateral surface of the lung, and there divides into an ascending and a descending superficial branch of small size; the others break up into parabronchia before reaching the surface of the lung.

9. The parabronchia are much wider in *Apteryx*, the diameters of their cavities varying from 1·5 millim. to 0·8 millim., while they range from 0·8 to 0·4 millim. in the Duck. Moreover the intervening vascular parenchyma is relatively much narrower in *Apteryx* than in the Duck. Hence a section of the lung of the former appears much more coarsely spongy than one of the latter. In the Duck, as in many other Carinate birds, the parenchyma around each parabronchial canal is defined by linear interspaces from that of adjacent parabronchia; and in transverse section these boundaries have a polygonal, usually hexagonal form. In *Apteryx*, the parenchyma

between the parabronchial tubes is continuous, and the intercapillary air-passages show no interruption.

In the Duck, as in most Carinatæ, the fossulæ lead into branching passages (intercellular passages of Rainey), which radiate towards the periphery of the area of parenchyma which belongs to each parabronchium, finally ending in the intercapillary passages. In *Apteryx*, the fossulæ are mere shallow pits which open at once into the intercapillary passages.

Thus the respiratory organs of *Apteryx* are thoroughly ornithic, differing from those of other birds chiefly in the greater width and smaller aggregate surface of the respiratory passages, in the rudimentary condition of the pneumatic sacs, and in the much greater strength of the pulmonary and septal aponeurotic expansions.

Neither in *Apteryx*, nor in any other bird, has either of these the slightest real resemblance to a Mammalian diaphragm. For, as has been seen, the heart lies altogether behind both, and the muscular digitations of the pulmonary aponeurosis are supplied by the intercostal nerves, the phrenic being absent. The vertical and oblique septa really answer to the fibrous tissue of the posterior and middle mediastinum in Mammals.

In this, as in all other cases, the meaning of ornithic peculiarities of structure is to be sought, not in Mammals, but in Reptiles. It is only among Reptiles that we meet with pneumatic bones similar to those of birds (Crocodilia, Pterosauria, Dinosauria), pulmonary air-sacs (Chamæleonidæ), and membranous expansions which are comparable to the septa in birds.

In Crocodiles, which approach birds in so many other ways, the resemblance is closest. As in birds, the liver lies between the stomach and the pericardium, and has a peculiar peritoneal investment shut off from the great sac of the abdomen ; and, as in the Ostrich, the whole circumference of the stomach is united by fibrous tissue with the parietes. A fibrous expansion extends from the vertebral column over the anterior face of the stomach, the liver, and the dorsal and front aspect of the pericardium, to the sternum and the parietes of the thorax, separating the thoraco-abdominal space into a respiratory and a cardio-abdominal cavity, and representing the oblique septum of the bird. The respiratory cavity is similarly divided into a right and left chamber by a very deep median septum, traversed from before backwards by the œsophagus, trachea, and pneumogastric nerves, and containing the aortic arches. Each of these chambers is occupied by one of the lungs, the mesial face of which is closely adherent to the septum, while the lateral face, though quite free,

naturally fits closely to the parietes. As there are no air-sacs, each chamber has only one story.

When the lung is distended, its dorsal margin extends far up on the sides of the bodies and arches of the vertebræ, the height of which seems to be related to this dorsal expansion of the lung.[1] A broad, thin muscle arises, on each side, from the anterior margin of the pubis; and its fibres pass forwards, diverging as they go, to be inserted into the ventral face of the posterior part of the pericardium and into the ventral and lateral parts of the fibrous capsule of the stomach, passing between that organ and the adherent posterior face of the liver, and being inserted into the fibrous aponeurosis which covers the anterior face of the stomach, and represents the oblique septum.

Each bronchus is continued directly backwards into a wide canal, which dilates into an oval sac-like cavity at the posterior end of the lung, representing the mesobronchium with the posterior air-sac in birds.

In the dorsal and mesial wall of the mesobronchium there are five or six apertures, which lead into as many canals, representing the entobronchia in birds. These pass, the anterior two almost directly forwards, and the others more or less obliquely, to the dorsal margin; and they lie quite superficially on the mesial face of the lung. The first is very much larger than the others, and ends in a dilatation at the anterior end of the lung. It is united with the second by transverse branches. Along the ventral margin of the lung there are four sac-like chambers, which communicate, in the case of the two anterior, with the entobronchia, and, in the case of the two posterior, with the mesobronchium. Finally, there are two very large canals, external to these, which communicate with the mesobronchium by large apertures in its dorsal wall, and give off branches to the outer face of the lung, representing the ectobronchial system of birds. The orifices with which the surfaces of all these canals, except the anterior half of the mesobronchium, are thickly set, lead into depressions, which are often so deep as to become cylindrical passages, simulating the parabronchia of birds.

Thus, notwithstanding all the points of difference, there is a fundamental resemblance between the respiratory organs of Birds and those of Crocodiles, pointing to some common form (doubtless exemplified by some of the extinct Dinosauria), of which both are modifications.

[1] It seems not improbable that the great height of the bodies and arches of the anterior thoracic vertebræ in some Dinosaurians may be connected with a similar modification of the lungs.

XXXII

ON SAPROLEGNIA IN RELATION TO THE SALMON DISEASE. Extracted from the Twenty-first Annual Report of H.M.'s Inspectors of Salmon Fisheries.

Quarterly Journal of Microscopical Science, vol. xxii., New Series, 1882, *pp.* 311–333.

IN willingly assenting to the proposal of the Editor of the *Quarterly Journal of Microscopical Science* that the following extract from Mr. Walpole's and my Report should appear in the Journal, I adopt their suggestion that I should take upon myself all responsibility for what is there written after the words, "The first symptoms of this disease," on p. 541. T. H. HUXLEY.

June 23, 1882.

THERE are two other matters on which it is necessary for us to treat before we close this report; one of these we need only refer to in a short paragraph; the other we propose to deal with in more detail.

In the first place, it is our duty to point out that the multiplication of salmon is seriously affected by the increase of pollution. Into the particulars of these pollutions it is not necessary for us to enter. A reference to the Appendix will show the many cases in which new pollutions have arisen, or old sources of pollution have done fresh damage during the last twelve months, and the few cases in which steps have been taken to render pollution harmless. We may say generally that the multiplication of fish is made more difficult in this way, and that some of the rivers which have hitherto been most productive are in perhaps the greatest danger from this cause. It is for Her Majesty's Government, rather than for ourselves, to consider

whether, under these circumstances, any steps are desirable for the purpose of remedying these pollutions. It is merely our duty to point out the danger which arises from them.

The second point to which we desire to draw attention is the remarkable outbreak of a disease among the salmon of many rivers. The disease was noticed originally in the autumn and spring of 1877 in two rivers, the Esk and the Nith, which flow into the Solway Firth. It soon spread to the Eden and other adjoining rivers. In the spring of 1879 it was observed in the Tweed, when it rapidly became very serious, and in 1880, when a Commission was appointed to investigate it, it had extended to the Nith, the Annan, the Esk, the Eden, the Cree, and the Dee, all flowing into the Solway Firth; to the Doon and the Ayr in Ayrshire; to the Derwent in Cumberland, the Lune in Lancashire, and to the Tweed. Since then the disease has broken out in the Seiont, the Ogwen, and the Conway in North Wales, and in the Tay and North Esk in Scotland.

We have very little doubt that the disease which first excited attention in 1877 had existed, at any rate in a sporadic form, for many years. It was stated in evidence before the late Commission that Dr. Crosbie, formerly surgeon to the "Challenger" expedition, carefully investigated a case of the disease so long ago as in 1852. His observations will be found in the Commissioners' Report, p. 44. Other witnesses similarly stated to the Commissioners that they had observed sporadic cases of the disease for years. We may add that we have recently understood from a lessee of fisheries on the North Esk that he had seen diseased fish, without recognising them as diseased, for very many years; and we have very little doubt that sporadic cases of the disease occur in almost every river.

The first symptom of this disease is the appearance of small greyish or ashy discolorations of the skin, usually upon those parts of the body which are devoid of scales, such as the top and sides of the head, the delicate valvular membrane on the inside of the jaws, the adipose fin, and the soft skin at the bases of the other fins. Where such discoloured patches occur on the scaly parts of the body the scales are hidden by a film, and it might readily be supposed that they had been detached. But if the discoloured film is gently washed or wiped off, the scales will be found beneath perfectly undisturbed. On the scaleless part of the body, also, the discoloured places often look as if they were the effect of bruises or abrasions, but careful examination of the skin fails to reveal any evidence of external injury.

The exact character of this affection of the skin may best be

observed in the recently formed isolated patches, not bigger than a sixpence, in which the disease appears on the soft integument of the head. Such a patch is usually nearly circular and has a well-defined margin separating it from the healthy skin. The central region of the patch is somewhat raised and more discoloured than the rest; and faint ridges may commonly be seen radiating from it, through the marginal zone, to the edge of the patch. A single patch of this character may be observed on a fresh-run fish, which from its activity, the excellent condition of its flesh, and the perfectly normal aspect of its internal organs, shows itself otherwise to be in full health.

When a patch of diseased skin has once appeared, it rapidly increases in size and runs into any other patches which may have appeared in its neighbourhood. The marginal zone, constantly extending into the healthy surrounding skin, retains its previous characters, while the ashy central part changes. It assumes the consistency of wet paper, and can be detached in flakes, like a slough, from the skin which it covers. If the subjacent surface is now examined, it will be found that the *epidermis*, or scarf-skin, has disappeared, and that the surface of the vascular and sensitive *derma*, or true skin, beneath is exposed. As the diseased area extends the papyraceous coat more and more completely takes the place of the epidermis, until, in extremely bad cases, it may invest the back and sides of a large salmon from snout to tail.

The affection, however, is not confined to the epidermis. As the patch acquires larger and larger dimensions the derma, or true skin, in its centre becomes subject to a process of ulceration; and thus a deep bleeding sore is formed, which eats down to the bones of the head and sends off burrowing passages, or sinuses, from its margins.

In severe cases the skin of the top of the head, of the snout, of the gill covers, and of the lower jaw, may be almost completely destroyed, and the affection may extend far into the interior of the mouth. Cases of the blinding of fish by extension of the disease over the eyes are reported. It is also said that the gills are attacked; but, although careful attention has been paid to this point, the gills have been unaffected in every fish that has come under our notice, however severe and extensive the disease might be. In far advanced cases the edges of the fins become ragged; and sometimes the skin which invests the fin rays is so completely destroyed that they stand out separately.

All observers agree that the flesh of a diseased salmon, however extensive the morbid affection may be, presents no difference in texture or in colour from that of a healthy fish; and those who have

made the experiment declare that the flavour of a diseased fish is as good as that of a healthy one. No morbid appearances are discoverable either in the viscera or in the blood. Moreover, when fresh-run fish are diseased they may exhibit just as large an accumulation of peritoneal fat as healthy fish. Nevertheless, it is certain that the cutaneous affection causes much irritation. The fish exhibit signs of great uneasiness, often dashing about and rubbing themselves against stones and other hard bodies in the water. Eventually they get weaker, become sluggish, and often seek the shallows before they die.

The disease spreads with great rapidity after it has commenced, three or four days being said to be sufficient to enable it to extend over the whole body of a large salmon.

In the early stages of the malady the peculiar appearance of the parts of the skin affected might readily be, and certainly often has been, ascribed to mechanical injury. It has already been remarked that the scales often appear to have been detached when in reality they are only hidden by the pellicle which covers them ; nor, so far as inspection with the naked eye goes, is there anything to suggest that the disease, in its most advanced form, is anything but a sloughing ulceration of the skin. But when the papyraceous substance which constitutes the apparent slough is subjected to microscopic examination, it proves to be something totally different from mere dead tissue of the fish, such as a true slough would be. In fact, the comparison with wet paper turns out to be more exactly correct than might have been anticipated ; for, like wet paper, it is chiefly composed of a felted mass of vegetable filaments, intermixed with which are *débris* of the tissues of the skin of the salmon and all sorts of accidental impurities, especially shells of Diatoms and multitudes of very minute sand grains, derived from the water in which the salmon swim. The filaments vary in thickness from $\frac{1}{600}$ of an inch to $\frac{1}{3000}$ of an inch, the majority lying between $\frac{1}{3000}$ and $\frac{1}{2000}$ of an inch. Each filament is tubular, composed of a thin wall, which contains cellulose, or the essential proximate principle of wood, lined by a thicker or thinner layer of finely granular protoplasm, within which, again, is a watery fluid. The whole filament is colourless and usually transparent, but sometimes the granules are sufficiently numerous to render it opaque, and then it looks white by reflected light. Sometimes the filaments are simple as far as they can be traced ; sometimes, on the other hand, they are much branched ; but they never exhibit any transverse partitions, the cavity of each filament being continuous throughout. Wherever the free end of a filament is to be seen it is rounded, closed, and often no

larger than the rest; or the filament may taper to its extremity. But the free ends of a greater or less number of the filaments are slightly enlarged, so as to be club-shaped, or they may be pyriform, or even almost spheroidal, and the layer of protoplasm which they contain is very thick. The cavities of some of these enlarged ends are shut off by a transverse partition from the rest of the filament, thus giving rise to a closed case. In others the protoplasm is broken up into a number, greater or less, according to the size of the enlargement, of equal-sized spherical masses, each rather less than $\frac{1}{2000}$ of an inch in diameter, which lie separate, but closely packed in the interior of the case, like shot in a cartridge (Fig. I, p. 545). In others the case is seen to be open at the end, and a portion or the whole of the "shot" have passed out. In yet others, again, a full unopened case is seen to lie inside an empty one.

The papyraceous mass is, in fact, what is known as the *mycelium* of a fungus. It answers exactly to the similar wet-paper like crust which is formed by the common fungus, *Penicillium glaucum* (usually known as "blue mould"), on the surface of a pot of jam. The filaments are the stems of the fungus, and are technically known as *hyphæ*. The enlarged ends of the hyphæ which are converted into the "cases," are the *sporangia*, or fruits of the fungus; and they are termed *zoosporangia*, inasmuch as the spheroidal bodies or *spores*, under certain circumstances, are actively locomotive after the fashion of many animalcules, and are, therefore, termed *zoospores*. It is a peculiarity of this particular fungus that, when a zoosporangium has emptied itself, the hypha on which it is supported begins to grow afresh, sends a prolongation through the centre of the empty sporangium, and dilates into a new one within or beyond it. Hence the appearance of a full sporangium, surrounded by one, or it may be two or three empty ones, one inside the other (Fig. II, p. 545).

This structural feature is peculiar to the genus *Saprolegnia* among fungi, and it enables mycologists to identify the fungus, of which the papyraceous incrustation characteristic of the salmon disease is a product, as a species of that genus.

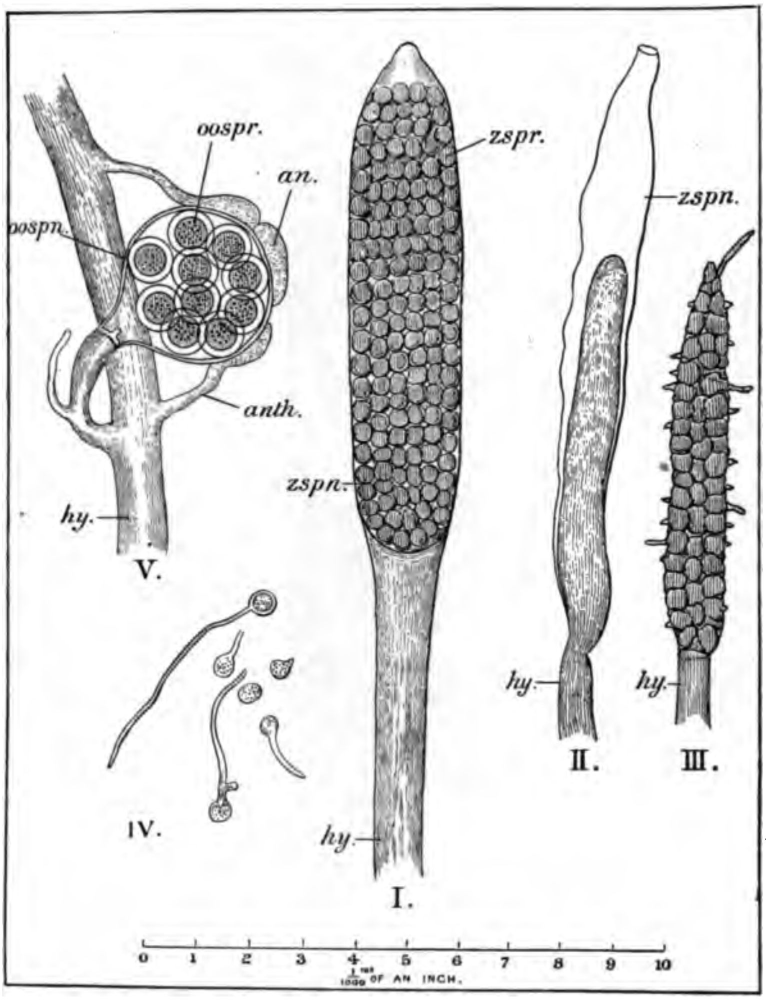
Thanks especially to the labours of Pringsheim,[1] Cornu,[2] De Bary,[3] and Brefeld,[4] a great amount of accurate information respecting the *Saprolegniæ* has been accumulated of late years.

[1] "Die Entwickelungs-geschichte der Achlya prolifera." Nova Acta, 1851, and several later papers in the 'Jahrbücher für Wissenschaftliche Botanik' for 1857, 1860, and 1874.

[2] 'Monographie Annales des Sciences Naturelles, Botanique,' 1872.

[3] De Bary and Woronin. "Untersuchungen über die Peronosporeen und Saprolegnien," 1881.

[4] 'Botanische Untersuchungen,' Heft iv, 1881, p. 109, 110.



Characteristic Forms of the Sporangia and Spores of Saprolegnia.

I.—A zoosporangium full of nearly ripe zoospores from the skin of a living diseased salmon.

II.—An empty zoosporangium, through the centre of which the hypha is growing in order to produce a new zoosporangium. From the fresh growth of *Saprolegnia* on the diseased jaw membrane of a salmon, cut off and placed in water.

III.—A dictyosporangium from salmon *Saprolegnia* cultivated on a dead fly. The spores have remained in the interior of the zoosporangium, and, after encasing themselves, have there germinated.

IV.—Zoospores of salmon *Saprolegnia*, germinating in water.

V.—An oosporangium of *Saprolegnia* from the pike, cultivated on a dead fly. The oosporangia of the salmon fungus in all respects resemble this.

Signification of the letters :—***hy***, hypha ; ***zspn***, zoosporangium ; ***zspr***, zoospore ; ***oospn***, oosporangium ; ***oospr***, oospore ; ***anth***, antheridial filament ; ***an***, antheridium.

They may be defined as a kind of water-moulds, which usually live at the expense of dead and submerged animal and vegetable substances, and are especially common upon dead insects and other invertebrate animals. Their delicate hyphæ form a white cottony fringe to such matters.[1]

A dead fly which has fallen into water is a favourite nidus for *Saprolegnia*, the hyphæ of which radiate from it in all directions, so that the fly appears to be enclosed in a pale white fluffy ball. Careful examination shows that such a fly represents the soil in which an immense number of the minute *Saprolegniæ* are implanted. One half of each fungus consists of branching hyphæ which answer, in a fashion, to the stem and branches of an ordinary plant, and are visible externally; the other half of the fungus corresponds, in the same general way, to the root and rootlets, the hyphæ ramifying in the interior of the fly, and the two parts being connected by a portion which traverses the dense cuticle with which a fly's body is coated.

The stem-hyphæ answer exactly in size and structure to the hyphæ of the salmon fungus. Moreover, a large number of them terminate in zoosporangia of the same character, which evacuate their zoospores, and are reproduced in the same way.

Flies, or parts of flies, such as the legs, on which *Saprolegniæ* are healthily growing, can be isolated and watched for any needful time under the microscope, so that the whole process of the formation of the zoosporangia and zoospores can be followed step by step. It may then be observed that the simple subcylindrical free end of a hypha enlarges, that protoplasm accumulates in it, and that its cavity, finally, becomes shut off by a transverse partition from the rest of the hypha, as a zoosporangium, the summit of which is usually slightly conical. The protoplasm is then seen to break up, simultaneously, into from eight or ten to a hundred and fifty zoospores, according to the size of the zoosporangium. The apex of the latter then opens and the zoosporangia are emitted. Each zoospore, as it leaves the zoosporangium, is usually in active motion, being propelled by the rapid lashing of two vibratile cilia which are attached to one point of its surface. After a few minutes it becomes quiescent and surrounds itself with an extremely delicate transparent coat. But this repose is of a very short duration, as it soon emerges from its envelope, and moves about even more actively than before. It has now an elongated oval shape, and has two cilia which proceed from one side of the oval. This second active state may last for a day, or perhaps two; and it is obvious that, from the activity of the motion of the

[1] Whence the name σαπρός, *sapros*, rotten, and λέγνον, *legnon*, the edging of a garment.

zoospores, to say nothing of accidental currents, they may be thus carried a long way from the parent stock. Sooner or later, however, they again come to a state of rest, which is final, and they then usually germinate. That is to say, one, or perhaps two, delicate filaments grow out and represent the primitive hyphæ of a new *Saprolegnia* (Fig. IV, p. 545).

If the spore has attached itself to some body which is incapable of affording it nourishment, it may not germinate at all, or, if it germinates, it speedily dies. But, if it falls upon an appropriate soil, such, for example, as the body of another dead fly, the spore sends a prolongation inwards which perforates the tough chitinous cuticle of the fly, and gives rise to a system of root-hyphæ in its interior; while, simultaneously, it grows outwards into a similarly ramifying stem-hypha, the branches of which soon enlarge into zoosporangia and give rise to zoospores, as before.

The growth and development of the *Saprolegnia* take place with extraordinary rapidity. In thirty-six hours from the first infection of the body of a dead fly with the *Saprolegnia* spores, it may be covered with a thick coat of stem-hyphæ a fifth of an inch long; and, in the course of the second or third day, a thousand of these may have developed and emptied their sporangia, thus setting free some 20,000 zoospores, every one of which is competent to set up the same process in a new fly-corpse. As all this production takes place at the expense of the tissue of the fly, the supply of nutritive material gradually diminishes. At about the fourth day, or perhaps not till later, new forms of sporangia, termed "dictyosporangia" (Fig. III, p. 545), in which the spores encase themselves and often germinate while still within the sporangium, make their appearance; and the ordinary zoosporangia diminish in number. Not unfrequently, about this time or subsequently, the hyphæ tend to break up into short joints which are themselves capable of germination. Finally, after the fifth or sixth day, a new kind of sporangium usually makes its appearance, which is termed an *Oosporangium*, inasmuch as the spores to which it gives rise are more like eggs, or seeds, than the products of the zoosporangia or those of the dictyosporangia.

The summit of a hypha, or a short branch of a hypha, dilates into a spheroidal sac, the cellulose wall of which becomes thickened, but presents, here and there, thin places, looking like clear circular dots, or apertures, under the microscope. Protoplasm accumulates in the spheroidal case thus formed; and either remains a single rounded mass, or divides into a smaller or greater number of spheroids, each of which, much larger than a single zoospore, is an *Oospore*. The

oospore, or oospores, thus formed eventually become invested by a thick cellulose coat. Before this happens, in some forms of *Saprolegnia*, slender twig-like branches are given off either from the stalk of the oosporangium or from an adjacent hypha, and the terminal portion of one or more of these twigs applies itself to the oosporangium. This terminal portion becomes shut off from the rest of the twig by a transverse septum, and is an *Antheridium*. The antheridium pierces the wall of the oosporangium, divides into as many branchlets as there are oospores, and one branchlet applies itself to each oospore. In all probability something passes from the antheridium into the oospore, and effects fecundation (Fig. V, p. 545).

Thus the oosporangium represents a female reproductive organ, and the oospore takes the place of an egg or an embryo cell. The antheridium represents a male organ, and its contents represent the essential substance of spermatozoids, or the fertilising matter of a pollen tube; and, after fecundation, the oospores answer to impregnated ova or fertilised seeds.

The oosporangium may burst and give exit to the oospores, or it may fall with them to the bottom. And, as a general rule, the oospores remain for a long time, sometimes several months, unchanged. Sooner or later, however, they germinate; and this process may take place in various ways:

1. The contents of the oospore may divide directly into locomotive zoospores which are set free.

2. The oospore may send out a hypha, the apical part of which becomes converted into a zoosporangium.

3. The oospore may send out a hypha, and this coming into contact with the body of a fly or some such matter, may develop into a mycelium in the ordinary way.

The whole series of phenomena now described represents the fullest set of changes known to occur in any one form of *Saprolegnia*. But, even in the same form, the series may present notable variations. Thus, the zoospores may germinate without passing into an active condition; or they may germinate immediately after they assume the first quiescent state. Again, in one and the same form, antheridia are sometimes developed and sometimes absent. In some forms, indeed, antheridia never make their appearance, and consequently fertilisation does not occur. Nevertheless, the unfertilised oospores germinate and produce new *Saprolegniæ* apparently just as well as if they were fertilised.

The commonest species of *Saprolegnia* has received the name of *S. ferax*, and both Pringsheim and De Bary agree that several

so-called species, namely, *S. monoica*, *S. thureti*, and *S. torulosa* are merely more or less permanent varieties of *S. ferax*; that they are all, in fact, members of the *S. ferax* group.

It has been seen that the fungus which grows on diseased salmon is unquestionably a species of the genus *Saprolegnia*; and it is commonly identified with *S. ferax*. But this identification has rested upon very slender grounds. It is practically almost impossible to determine the species of a *Saprolegnia* until the characters of its oosporangia and of its antheridia (if it have any) have been accurately made out. At present not only are we without any sufficient account of these organs in the salmon *Saprolegnia*, but it is certain that they are, at most seasons, extremely rare. Mr. Stirling[1] speaks of having observed only four in the course of all his investigations; and not a single specimen has presented itself in the considerable number of diseased salmon from the Conway, the Tweed, and the North Esk, which have come under our observation during the last four months.

When our inquiries commenced there was, strictly speaking, no proof that the salmon *Saprolegnia* could live on anything but a salmon. It was therefore quite possible that, since there are many species of *Saprolegnia*, that of the salmon might be peculiar to it, just as, in the analogous case of the potato disease, *Peronospora infestans* is different from all the species of *Peronospora* which abound upon European wild plants, and will not live on them, any more than these other species will live on the potato.

However this may be, it is easily proved that the *Saprolegnia* is not dependent on living salmon. In fact, if a patch of diseased skin is cut off and placed in a vessel of water, it will be found, in twenty-four hours, to be covered with a new growth of young hyphæ, close set and of nearly equal lengths, so that the surface resembles a miniature cornfield. A piece of the diseased membranous valve of the mouth of a salmon was placed in water on the 4th of March, 1882; on the 6th it was covered with young hyphæ one fifth of an inch long; and on the 7th these had elongated and developed multitudes of zoosporangia.

[1] Mr. Stirling's valuable contributions to our knowledge oi the salmon disease are contained in the 'Proceedings of the Royal Society of Edinburgh' for 1878 and 1879. Mr. W. G. Smith, in a paper on the salmon disease in the 'Gardener's Chronicle,' May 4, 1878, not only affirms that "the resting spores are common enough," but figures them. However, Mr. Smith's figures oi the zoosporangia are so unlike anything ordinarily observed in the salmon *Saprolegnia*, and his statement that "the fungus has invariably vanished with the death of the fish," is so strangely contrary to common experience, that it is difficult to know how much weight ought to be attached to his observations.

Moreover, there is not the least difficulty in proving that the salmon *Saprolegnia* is not dependant on salmon at all, but that it is capable of living on dead insects and pieces of wet bladder. If a recently killed fly is gently rubbed two or three times either over a fresh patch of diseased salmon skin, or over one which has developed the fresh growth just mentioned, and then placed in a vessel of water by itself, it will be found, in the course of eight-and-forty hours, to be more or less extensively beset with short, delicate, cottony-looking filaments, which rapidly increase in length and in number until, at last, the fly's body is enclosed within a spheroidal coat half an inch in diameter. These filaments are hyphæ having exactly the same size, form, and structure as those of the salmon *Saprolegnia*; their ends give rise to zoosporangia of the same character; and these produce zoospores of the same size, which germinate in the same way.

Between December, 1881, and April of the present year, repeated experiments of this kind have been made with diseased salmon from the Conway, the Tweed, and the North Esk, upon dead flies and small pieces of wet bladder, always with the same result. There appears, therefore, to be no doubt that the *Saprolegnia* of the salmon, like other *Saprolegniæ*, is capable of living and flourishing on a variety of dead animal matters.

When the *Saprolegnia* is established on one such substance it is easy to transmit it to another. The *Saprolegnia* obtained from diseased salmon was thus cultivated for many weeks (from the end of December, 1881, to the first week in April, 1882) in the hope of obtaining the oosporangia and thus identifying it with one or other of the described forms of the *S. ferax* group. Up to the last-mentioned date, however, no oosporangia appeared on any of these cultures. The course of events was this: for two or three days zoosporangia were very abundant, and thousands of zoospores were set free. But, in no case which came under observation, for several months, were these zoospores provided with cilia, or actively locomotive. They were discharged from the zoosporangia as simple spherical corpuscles, which flowed passively away, and were very often seen germinating by sending out a single delicate hypha. Immense numbers of these spores accumulated among the hyphæ.[1]

[1] Among previous observers, Mr. Stirling and Mr. W. G. Smith describe and figure locomotive zoospores as if they were of ordinary occurrence. Mr. Brook, on the other hand ("Notes on the Salmon Disease in the Esk and Eden," 'Transactions of the Botanical Society of Edinburgh,' 1879), appears never to have seen locomotive zoospores; and Mr. George Murray, of the Botanical Department of the British Museum, who has been kind enough to make a series of observations and experiments, continued over six or seven weeks,

After this condition had lasted for a day or two, the ordinary zoosporangia diminished in number, and "dictyosporangia" made their appearance in place of them. In other words, the spores instead of being discharged, were retained within the zoosporangium, and began to germinate in that position.

At the same time the protoplasm accumulated in certain regions of the hyphæ, which often became swollen, and these accumulations were shut off from the rest by transverse partitions. The hyphæ thus assumed a jointed or beaded appearance, as in the *S. torulosa* of De Bary, and the joints might eventually separate from the intervening empty parts of the hyphæ as a sort of buds or *gemmæ*, which, after detachment, might begin to germinate by throwing out delicate hyphæ at one or many points. Sometimes these buds were terminal and spheroidal and closely simulated oosporangia, but they did not give rise to oospores. No trace of antheridial branchlets was ever visible.

In the third week of April, however, oosporangia and antheridia, in all respects similar to those of the "*monoica*" form of *Saprolegnia ferax*, made their appearance in a copious growth of the fungus on a fly, which was infected on the 24th of March from a culture on bladder, which was again derived from a fly infected directly from a North Esk salmon on the 14th of March.

It may be safely concluded, therefore, that the salmon fungus is not a parasite peculiar to that fish, but that it is a form of the *Saprolegnia ferax*, which, so far as our observations go—and it must be remembered that these extend over only the quarter of the year between Christmas and the spring equinox—remains devoid of oosporangia so long as it infests the fish, and tends to persist in this condition for a long time, even when it is cultivated on those matters upon which the *Saprolegnia* more usually subsists. Future observation must determine whether oosporangia are developed on the *Saprolegnia*, while still growing on salmon, later in the year. The evidence of the fact at present extant is extremely unsatisfactory; and it is a remarkable circumstance that the figures which have been published show no trace of antheridial filaments.

That living fish may be attacked and destroyed by epidemic diseases, of which a *Saprolegnia* is either the cause or the constant accompaniment, has been known for a very long time.

on crops of *Saprolegnia*, raised upon dead flies infected from Conway salmon, has met with the same negative results. Quite recently, however (March 16), locomotive zoospores have been emitted from one of our specimens of salmon fungus cultivated on bladder. But, as in our specimens, so in those cultivated by Mr. Murray, no trace of oosporangia had appeared up to that time.

Forty years ago the eminent German botanist, Unger,[1] described a disease which broke out among some carp in a pond in the Botanic Gardens at Gratz, and was obviously caused by a fungus, at that time known as *Achlya prolifera*, but which the description and figures given by Unger clearly prove to belong to the genus which is now distinguished as *Saprolegnia*, and, indeed, to be very similar to, if not identical with, *S. ferax*. More or less distinctly circumscribed pale spots appeared upon the skin of the back and of the fins. The fish became sluggish and sought the surface of the water. A velvety investment, formed of very delicate, colourless, close-set threads, showed itself on the spots affected, which rapidly became confluent, and extended from mouth to anus, and even on to the gills. The scales of the affected parts became detached, red, and swollen, and sometimes ulceration occurred. The animals could no longer move without appearing to suffer great pain; they remained at the surface of the water, lying either on their backs or on their sides, and death took place in eight-and-forty hours. Unger found that the disease could be transferred to perch by inoculation.

Again, there seems no reason to doubt that the fungus which accompanied the epidemic disease affecting roach, dace, gudgeon, small pike, and perch, at Ightham in Kent, of which a very full and interesting account is given by Mr. Stirling,[2] is to be referred to *Saprolegnia ferax*. Here, however, ulcerative destruction of the skin does not appear to have occurred, and the mortality is said to have arisen from suffocation, the fungus obstructing the respiratory passages.

Pike kept in aquaria not unfrequently become covered with a fungus. The fish do not appear to be inconvenienced, and the fungus is very easily washed off. In a case of this kind, which we recently examined, the fungus was a *Saprolegnia*, the mycelium and the zoosporangia of which were altogether indistinguishable from those of the salmon fungus. Moreover, the hyphæ burrowed in the epidermis and distorted the cells with which they came in contact in just the fashion described below. As it was not desirable to kill the fish, it was impossible to determine whether the derma was penetrated or not; but the absence of sores and the ease with which large flakes of epidermis, in which the *Saprolegnia* was rooted, could be detached, lead to the conclusion that the *Saprolegnia* had not penetrated beyond the epidermis. The zoosporangia of the *Sapro-*

[1] "Sur l'Achyla prolifera," 'Annales des Sciences Naturelles, Botanique,' serie iii, 1844.

[2] "Additional Observations on Fungus Disease of Salmon and other Fish," 'Proceedings of the Royal Society of Edinburgh,' x, 1879.

legnia taken from the fish emitted actively locomotive zoospores, but no oosporangia could be detected.

Dead flies infected with this *Saprolegnia* on the 18th of March, 1882, yielded an abundant growth, quite similar to that obtained in the same way from the salmon *Saprolegnia* ; and on the 24th, that is, in six days, the characteristic oosporangia and antheridia of *Saprolegnia ferax* (*monoica*) made their appearance.

It appears, therefore, that *Saprolegnia ferax* is capable of attacking a great variety of fishes during life, but that the concomitant pathological phenomena differ in different fishes.

Mr. Stirling's experiments on the transmissibility of the salmon fungus to other fish yielded only negative results. Diseased salmon skin was put into a vessel containing minnows, which nibbled the skin, and were none the worse. Experiments of this rough-and-ready sort, however, really prove nothing ; and a great deal of light will assuredly be thrown upon the whole question of the salmon disease by carefully conducted experimental investigations.

At the present moment, we possess evidence that at least three distinct affections of the skin of fresh-water fishes have been confounded together under the name of "Aquarium fungus." One of these is associated with a *Saprolegnia* identical with that which attacks salmon ; another is attended by the very closely allied fungus, *Achlya* ; while the third is not accompanied by the growth of any fungus, but is a very curious morbid affection of the skin itself, apparently allied to epithelioma. We have hitherto observed it only in carp, the head, body, and fins of which sometimes appear covered with white patches, which present a most deceptive resemblance to those caused by *Saprolegnia*, the more especially as the edges of the fins may be eroded, and ragged fragments hang from the white patches. These patches, however, contain no fungus, but result from the abnormal growth of the epidermis, sometimes to eight or ten times its ordinary thickness, not unfrequently accompanied by a corresponding elongation of the papillæ of the derma.

Having thus dealt with the question of the nature and affinities of the fungus which is the constant concomitant of the "salmon disease," the next point for consideration is the relation of the fungus to the affection of the skin. Is the growth of the fungus the cause of that affection, or does the fungus merely find a favourable nidus in the production of the affection?

The *Saprolegniæ*, as we have seen, habitually grow on dead animal and vegetable substances ; and it is therefore a fair supposition that some morbid affection may cause the local death of the skin of

the fish ; and that the fungus simply implants itself in the dead tissue, as if it were the dead body of a fly.

On the other hand, our knowledge of the destructive epidemics caused by *Empusa* in flies, *Botrytis* in silkworms, and *Entomophthora* in other caterpillars, and of the multifarious fungi which produce bunt, smut, and mildew in plants, affords at least equal ground for the supposition that the ulceration and destruction of the skin are caused by the invasion of healthy fish by the *Saprolegnia*. The decision of this question is obviously of the greatest importance.

Direct experimentation by infection of healthy salmon in the manner in which dead flies were infected from the diseased salmon being out of the question at present on account of its practical difficulties, the only profitable way of investigation lay in the study of the minute structure of the healthy and of the diseased skin, so as to ascertain the exact relation of the fungus to the morbid appearances.

The skin of the salmon, like that of vertebrated animals in general, consist of a superficial, cellular, non-vascular scarf-skin, or *epidermis*, covering a deep fibrous and vascular true skin, or *derma*. The former is divisible into a superficial, a middle, and a deep layer of cells, the last being in immediate contact with the derma. The deep cells are vertically elongated, the middle ones more or less broadly spindle-shaped or rounded, while the thin superficial layer consists of flattened cells. The deep cells are constantly multiplying by fission, and their progeny become middle cells, the outermost of which, for the most part, becoming flattened, give rise to the superficial layer, which is continually shed and replaced. Some of the cells of the middle layer, however, enlarge, take on a more or less spheroidal form, and become filled with a mucous fluid. As they rise to the surface, they open and pour out this fluid, which lubricates the surface of the fish. In any vertical section of a properly prepared portion of salmon skin more or fewer of the openings of these cells are to be seen. The derma is composed of matted bundles of connective tissue, traversed by blood-vessels and nerves, and containing numerous lymphatic spaces. The superficial layer of the derma contains a number of dark pigment cells, of which there is a close-set zone immediately beneath the epidermis.

In a thin vertical section of the skin of the head of a salmon, which has passed from the sound skin through the centre of a diseased patch, the various structural elements which have been described, disposed with great regularity, are alone visible in the healthy part of the section. But, on advancing within the margin of

the diseased area, hyphæ of the *Saprolegnia* are seen to penetrate horizontally between the cells of the middle layer, thrusting them asunder with so much force that the cells become bent and distorted, and adhere to a hypha as if they were spitted on it. And, in fact, it is because bundles of such hyphæ are thrusting themselves in this manner, as the roots of an ordinary plant thrust themselves into the soil, between the epidermic cells, that the radiating ridges which appear on the marginal area of the diseased patch are formed. Close up to the free ends of these hyphæ, however, the epidermis is perfectly healthy; and this fact suffices to prove that the growth of the fungus is the cause of the morbid affection of the epidermis, and not its consequence.

Proceeding further towards the centre of the diseased patch, the hyphæ become more numerous and take a vertical as well as a horizontal direction. Of the vertical ones, some traverse the epidermis outwards, thrusting aside and disturbing its cells, and terminating in short free ends on the surface. Others of the vertical hyphæ, on the contrary, are directed inwards; and, as root-hyphæ, not only traverse the deep layer of the epidermis, but pierce the superficial layer of the derma, and penetrate into its substance for a short distance. Yet nearer the centre the epidermis is completely broken up into fragments and detached cells, which lie in the meshes of the thick mycelium formed by the horizontal and vertical stem-hyphæ of the fungus. The vertical stem-hyphæ attain their full length, often branching, and begin to develop zoosporangia. Towards the derma the root-hyphæ are so numerous and close set that they are often separated by interspaces which hardly exceed their own diameter where they penetrate the superficial layer of the derma. Moreover, they branch out in the latter to a depth of a tenth of an inch, often penetrating the bundles of connective tissue. Their ultimate ramifications usually end in curiously swollen extremities. Still more towards the centre of an ulcerated patch, the place of the epidermis is taken by the felted mycelium of the *Saprolegnia*, the superficial layer of the derma has disappeared, small vessels have often been laid open, and blood has been effused.

All these appearances become perfectly intelligible if we suppose that, when *Saprolegnia* spores reach the surface of the body of a live salmon, they behave in the same manner as we know they do when they reach the surface of the body of a dead fly. If it should light upon one of the apertures of the mucous cells an easy road into the soft interior of the epidermis is open to the hypha of the germinating spore. But, apart from this, the flat superficial cells are certainly as

easy to pierce as is the tough cuticle of a fly. No doubt, as in the fly, the hypha grows directly inwards, and piercing the superficial layer of the derma, comes into direct relation with the abundant nutriment it finds there. The fungus then ramifies, on the one side, in the derma, on the other in the epidermis, sending off in the latter vertical branches which soon develop sporangia, and horizontal branches, which are driven, like subsoil ploughs, into the middle layer of cells. The zoosporangia emit multitudes of zoospores, many of which are deposited on the epidermis in the neighbourhood of the first; and, penetrating it in the same way, add to the *Saprolegnia* plantation. Thus the disease constantly spreads centrifugally; and, as the oldest and most luxuriant growth of *Saprolegnia* is in the centre, so is the mechanical destruction of the epidermis first effected there. But it is in this region also that the greatest number of root-hyphæ penetrate the derma. They cannot fail to interfere with the nutrition of the tissues which they traverse; in fact, their ramifications are often so close set that the proper tissues of the superficial layer of the derma almost disappear. Sooner or later, therefore, necrosis sets in, and then ulcerative sloughing takes place, resulting in an open sore. No doubt the morbid process thus described is accelerated and intensified by the irritation caused by the innumerable small grains of sand and other foreign bodies entangled by the mycelium. But that the primary cause of all the mischief is the parasitic fungus does not appear to be open to doubt. If it were otherwise, the structural alteration of the skin should precede the fungus, and not follow it, as it actually does.

In fact, the *Saprolegnia* is the cause of the salmon disease exactly as the closely allied fungus, *Peronospora*, is the cause of the potato disease. In symptoms, progress, and results there is the closest analogy between the two maladies. *Peronospora*, like *Saprolegnia*, gives rise to spores which may be ciliated and actively locomotive, or may germinate without passing through an active stage. When these spores germinate on the surface of a healthy potato plant, their hyphæ perforate the walls of the cells with which they are in contact, and then ramify, as a mycelium, in the inner substance of the plant, carrying destruction wherever they go. The mycelium gives off hyphæ which pass through the stomates to the surface, and there they throw off abundant spores, which repeat the process until the whole plant is destroyed. Even the tubers are invaded; but in them the mycelium becomes quiescent on the approach of the winter season, to break out again, in full vigour, if the tubers are planted in the following spring. Moreover, there is as much uncertainty about

the occurrence of antheridia and oosporangia, and of any sexual method of reproduction in the *Peronospora* of the potato, as in the *Saprolegnia* while it infests the salmon.

There is a great deal of reason to believe that the *Saprolegnia* growing on salmon is killed by salt water; and that the injured skin may heal and become covered with a new epidermis when a diseased salmon enters the sea. But the discovery that the root-hyphæ of the *Saprolegnia* ramify in the derma where the sea water cannot reach them, raises a curious and important question. It becomes possible that a diseased salmon returning to the sea may regain a healthy epidermis and appear perfectly sound; but that, like a potato-tuber invaded by *Peronospora* just before the approach of winter, the fungus in the derma may simply lie dormant, and be ready to spring into activity as soon as the fish returns to fresh water. Cases of the appearance of the disease in quite fresh-run fish are occasionally reported, which would be readily explicable should this supposition turn out to be well founded.

Another possibility was suggested by the same fact. We know that the spores of the *Empusa*, a fungus which attacks living flies, germinate and bore through the cuticle in much the same fashion as the *Saprolegnia* enters dead flies. But the hypha of the *Empusa*, which has thus entered the fly, immediately breaks up into short joints, which diffuse themselves through the body of the fly and everywhere multiply by division, until they have appropriated all the nutritious matters which are available to them. It was therefore justifiable, on analogical grounds, to suppose that the hyphæ of *Saprolegnia*, which had entered the derma of a salmon, might break up in a similar way; and that the segments might be conveyed through the lymphatic and blood-vessels into all parts of the body, and either produce blood poisoning by a septic fermentative action, or develop centres of obstruction by lodgment in the narrower channels of the vascular system. However, there is no evidence to justify this suspicion. The hyphæ in the derma show no signs of division, nor have any toruloid bodies or other structures that can be regarded as derivates of *Saprolegnia* been observed, either in the blood or in any of the viscera.

The salmon disease, in fact, appears to be a purely cutaneous affection; and the fish seem to die partly from irritation and consequent exhaustion, and partly, perhaps, from the drain on their resources, caused by the production of so large a mass of vegetable matter at their expense.

The opportunities for the investigations, the chief results of which

have now been detailed, have arisen only during the last three or four months ; and a great deal more time and attention must be devoted to the subject before it can be expected that many of the obscurities and difficulties which still hang about it can be cleared up.

It is needful to discover the conditions under which the fungus exists in those rivers which are infested by the disease when the full-grown salmon have deserted them ; whether it lingers in isolated cases among the parr, trout, or the non-salmonoid fish ; or whether it contents itself with the bodies of dead insects and other dead animal, and perhaps vegetable, substances ; or whether, in the late summer, oosporangia may not be formed and give rise to oospores, which, as De Bary's experiments show, may have a dormant period of three or four months, that is to say, sufficient to preserve them till the next return of the salmon.

On all these points persons conversant with the use of the microscope, who are resident in the neighbourhood of salmon streams, might obtain information of great value, hardly to be procured in any other way.

Although all the evidence leads to the conclusion that the *Saprolegnia* is the immediate and primary cause of the salmon disease, and that, in the absence of the fungus, the disease never makes its appearance, however polluted the water may be, or however closely the fish may be crowded ; yet, in this, as in other epidemics caused by parasitic organisms, the prevalence and the mortality of the malady, at any given time and in any given place, must be determined by a multitude of secondary conditions independent of the immediate cause of the disease.

In the case of the potato disease it is well known that dry weather is extremely unfavourable to the growth and diffusion of the *Peronospora*. In such a season a plant may be affected here or there, but cases of disease are so rare that they escape notice. But, if even a few days of rain with a thoroughly damp atmosphere supervene, the fungus spreads from plant to plant with extraordinary rapidity, and field after field is devastated as if struck by a sudden blight. So with the epidemic disorders of mankind. In a large town isolated cases of smallpox, measles, diphtheria, and the like, constantly occur, and every case is the source of a vast quantity of infectious material. Nevertheless, it is only under certain conditions that this infectious material takes effect and gives rise to an epidemic.

At a moderate estimate the *Saprolegniæ* on a single dead fly may carry a thousand zoosporangia. If each sporangium contains twenty zoospores, and runs through the whole course of its development in

twelve hours, the result will be the production of 40,000 zoospores in the course of a day, which is a number more than sufficient to furnish one zoospore to the cubic inch of twenty cubic feet of water. Even if we halve this rate of production it is easy to see that the *Saprolegniæ* on a single fly may yield a sufficient abundance of zoospores to render any small and shallow stream, such as salmon often ascend for spawning purposes, dangerous for several days. For a single one of these spores, if it adheres to the surface of the skin of a salmon and germinates, is sufficient to establish the disease. Other things being alike, of course the greater the quantity of *Saprolegnia* in a stream the greater the chances of infection for the fish which enter it.

In looking for the causes of an epidemic of salmon disease we have, therefore, to inquire, in the first place, into the conditions which favour the growth of the *Saprolegnia.* It is known that the *Saprolegniæ* subsist, not only on dead insects and on dead crustacea and molluscs, but on some other dead animal matters and on decaying plants. The particular form which infests the salmon, as we have seen, flourishes as well upon dead flies ; it can also be grown upon pieces of bladder, but whether it can be transferred to decaying vegetable substances has yet to be determined.

Hence it follows that, within certain limits (active putrefaction appearing to be unfavourable to *Saprolegnia*), an increase of the quantity of dead insects and other such organic matters in a river must tend to favour the growth and multiplication of any *Saprolegniæ* which it contains, and hence to increase the liability to infection of the salmon which ascend it.

And that this is no mere hypothetical deduction is very well shown by a remarkable case which was carefully investigated by Goeppert [1] nearly thirty years ago.

A peculiar water-mould, commonly known as *Leptomitus lacteus*, but which is so closely allied to *Saprolegnia* that Pringsheim places it in that genus, is widely spread in running waters, where it grows on all sorts of dead organic substances.

A factory for making spirit from turnips was established near Schweidnitz, in Silesia, and the refuse was poured into an affluent of the River Westritz, which runs by Schweidnitz. The result was such a prodigious growth of *Leptomitus* that the fungus covered some 10,000 square feet at the bottom of the stream with a thick white layer, compared to sheep's fleeces, choked up the pipes, and rendered

[1] 'Botanische Zeitung,' xi, p. 163, 1853.

the water of the town undrinkable. Scattered hyphæ of this *Leptomitus* may sometimes be found among those of *Saprolegnia* growing on fresh-water fishes; and the two forms are altogether so similar, that conditions analogous to these which stimulate the growth of the one may safely be assumed to favour that of the other.

Brefeld has pointed out that there is no better medium for the culture of fungi of all sorts than an infusion of dung ("mistdecoct"). Land under high cultivation undoubtedly supplies the waters in its neighbourhood with something that nearly answers to an infusion of dung; and this must be taken into account in discussing the possible factors of salmon disease.

Again, it is known with respect to many of the common moulds, such as *Penicillium* and *Mucor*, which are habitually *saprophytes* (that is to say, live on decaying organic matter, as *Saprolegnia* does), that they flourish in certain artificial solutions containing salts of ammonia. It is quite possible, though whether the fact is so will have to be experimentally determined, that *Saprolegnia* is capable of living under the same conditions. Fungi are also extremely sensitive to slight differences in the acidity or alkalinity of water, so that even apparently insignificant changes in this respect may come into play as secondary conditions of salmon disease. Hence, although there is not the slightest ground for regarding "pollutions," whether they arise from agricultural or from manufacturing industries, as primary causes of salmon disease, they may have a most important secondary influence; they may, in fact, determine whether, in any river, the disease shall be sporadic or epidemic.

But of all the conditions which determine the increase of *Saprolegnia*, and therefore multiply the chances of infection of healthy fish, the presence of already diseased fish is obviously one of the most important. A large fully diseased salmon may have as much as two square feet of its skin thickly covered with *Saprolegnia*, and its crop of spores may be taken as equivalent to that of several hundred flies. It may be safely assumed that forty such salmon might furnish one spore to the gallon for all the water of the Thames which flows over Teddington Weir (380,000,000 gallons) in the course of a day.

In 1878, 350 dead salmon were taken out of a very small river, the Esk,[1] in three days. If the zoospores which these gave off had been evenly diffused through the water of the Esk, the

[1] Stirling, 'Proceedings of Royal Society of Edinburgh,' vol. ix, p. 726.

difficulty is to understand how any fish entering it could escape infection.

In fact the objection easily arises that these arguments prove too much; and that, if the *Saprolegnia* is the cause of the disease and its spores thus widely diffused in an infected river, not a fish which ascends that river should escape the disease.

But such an objection loses its force if it is remembered that, though the *Saprolegnia* is the cause of the disease, and though a single spore is undoubtedly sufficient to kill a salmon, yet, in order to produce that effect, the spore must, in the first place, reach and adhere to the epidermis of the salmon; in the second place, it must germinate; and, in the third place, the delicate hypha which it sends out must bore its way through the epidermis into the derma.

Each of these conditions of successful infection may be modified in endless ways of which we know nothing—by the state of the epidermis of the fish; by the motility and the general vital energy of the spore; by the composition of the water, and especially by that of its gaseous and acid or alkaline contents.

To take only one of these conditions. If the spores germinate within the zoosporangia, or are not locomotive after they leave it their chances of diffusion, and hence of receiving a healthy fish, will be vastly less than if they are locomotive, for even a short time. And, again, their chances will be far less if they germinate after the first locomotive state, which lasts only a few minutes, than if they enter into the second locomotive state, which may endure for four-and-twenty hours or more. So, if the salmon *Saprolegnia* produces oosporangia in the late summer, and these lie dormant at the bottom until the following spring, the chances of infection of fresh-run fish will be greater than they will be if the continuance of the existence of the *Saprolegnia* through the winter depends upon the accident of a sufficient supply of dead organic substances.

Moreover, any one who has practised the cultivation of *Saprolegnia* is familiar with the difficulties which arise from the swarms of *Infusoria* and *Bacteria* which devour, or otherwise destroy, the fungus, notwithstanding all his efforts to preserve it.

The struggle for existence rages among fungi as elsewhere; and the question whether a salmon which enters water in which *Saprolegnia* is present shall be infected or not depends upon the mutual adjustment of a vast variety of conflicting agencies. Until we have learned something more than we at present know of these agencies,

and of the history of the salmon *Saprolegnia* itself, there can be no thoroughly safe foundation for any view which may be put forward as to the best mode of dealing with the disease.

Nevertheless, since it is evident that every diseased salmon which remains in a river must immensely increase the chances of the infection of the healthy fish in that river, the policy of extirpating every diseased fish appears, theoretically, to be fully justified. But whether, in endeavouring to carry such a policy into effect in any given river, the cost would not exceed the loss from the disease, is a point which must be left for the consideration of Boards of Conservators.

XXXIII

1. CONTRIBUTIONS TO MORPHOLOGY. ICHTHYOPSIDA. —No. 2. ON THE OVIDUCTS OF *OSMERUS*; WITH REMARKS ON THE RELATIONS OF THE TELEOSTEAN WITH THE GANOID FISHES.

Proceedings of the Scientific Meetings of the Zoological Society of London for the Year 1883. *pp.* 132–139. (*Read March 20th,* 1883.)

NEARLY sixty years ago, one of the most accurate and prolific of modern anatomists and embryologists, Rathke, published a memoir on the alimentary canal and the reproductive organs of fishes,[1] which is not the least valuable of its author's numerous and weighty contributions to science. At p. 122 Rathke writes:—"In certain fishes the oviducts have entirely disappeared; this is the case in the Eel, in the Sturgeon,[2] in *Cobitis tænia*, and in the Lamprey. In others, however, such as the higher kinds of Salmonoids, there extends back, behind each ovary, a narrow band which may be regarded as the remains of an oviduct. In all these fishes, therefore, the central abdominal cavity must take the place of the oviduct, as it receives the eggs when they are detached, and allows them to make their exit by a single opening at its posterior extremity.

"In the Smelts (*Stinten*), however, there passes from each ovary a band, one edge of which is attached to the dorsal, the other to the abdominal wall, so that, in each lateral half of the abdominal cavity,

[1] H. Rathke, "Ueber den Darmkanal und die Zeugungsorgane der Fische," Schriften der naturforschenden Gesellschaft zu Danzig, Heft iii. Band 24.

[2] Rathke, taking the structure of ordinary osseous fish as his standard, says justly enough that the "oviducts [such as these fish possess] have disappeared" in the Sturgeon. In *Cobitis barbatula* the single ovary has an oviduct of the same character as in other Cyprinoid fishes. I have not examined *C. tænia*, about which, in other parts of his memoir, Rathke's statements are full and precise.

there is a chamber which receives the eggs when they are detached from the ovary. The two chambers ultimately unite above the anus ; and, in fact, close in front of the place where, in other fishes, the oviduct is situated.

"Thus the Smelts appear to present a remarkable transition to that structure of the oviduct which alone is met with in the other classes of the Vertebrata. Instead of the oviduct having, as in these, the character of an independent tube, in the Smelts only one half of it is found, and yet this has united in such a way with the wall of the abdominal cavity that a part of this wall takes the place of the other half of the oviduct."

And, further, at page 159 :—

"That a proper oviduct is absent in the Salmon tribe has already been stated, and also that they possess an analogue of that structure. This consists of a flat, narrow band, which commonly arises at the upper and posterior end of the plate-like ovary, gradually diminishes in width backwards, and finally becomes lost towards the end of the abdominal cavity. In the Salmon proper it disappears upon the air-bladder, opposite the commencement of the last fifth of the abdominal cavity, in the freshwater Trout on the sides of the intestine not far from the anus, in the *Coregoni* (Maränen) on the intestine close to its end.

"The transition from this band-like membranous process of the ovaries of the higher Salmonoids to the oviduct of most fishes is remarkably exemplified in the Smelts. In these, in fact, a delicate membranous process, a mere fold of the peritoneum, proceeds from the end of each ovary, the upper edge of which is attached to the renal organ, the lower to the wall of the abdomen. In this way a cavity lies behind each ovary, bounded externally by the wall of the abdomen, and internally by this band. When the eggs are detached they fall into these cavities, which become narrower behind, and leave the body by a common aperture which lies behind the anus. The end of the intestine lies between the two cavities ; and since the left ovary lies far from the posterior end of the abdominal cavity, the singular oviduct which has just been described has, on the left side, a considerable length ; the right oviduct, however, is very short, the right ovary being situated so far back."

Rathke finally observes (p. 160) that he does not consider the condition of the ovaries in the Salmonoids, Eels, and Lampreys to represent the lowest condition of these parts in fishes, but rather to result from the subdivision of the reproductive organ into two separate parts—the one productive, and the other educative.

I am not aware that, since Rathke wrote, any one has paid attention to the remarkable arrangement which he describes; and though I have often intended to look into the matter myself, it is only lately that I have carried my design into effect.

As might be expected, I have found Rathke's statements, so far as the matters of fact are concerned, perfectly accurate.

Between the latter part of January and the beginning of March of this year I have examined a number of female Smelts, and always with the same results. I may remark that the ovaries were fully developed in the former month, and that, in the first week of March, four Smelts which I obtained in very fresh condition were all females, full of detached ova and ready to spawn.

The abdominal cavity of a female Smelt, in this state, is distended by a mass of ova, which are closely compacted and coherent, but become readily detached from one another when the mass is gently agitated in water or other fluid.

When the abdominal wall of the fish is carefully slit open along the ventral median line, the mass of impacted ova has almost the appearance of a vast single ovary; and, indeed, Bloch appears to have been misled by this appearance (Rathke, *l.c.* p. 132). But it may be readily broken up and washed away; and the two ovaries are then seen, one on each side of the middle line—not opposite one another, however, but the left in the anterior, and the right in the posterior half of the abdominal cavity[1] (fig. 1, p. 135). Each ovary has the form of a half-oval plate, with the curved edge ventral and the straight edge dorsal. The latter is suspended by a narrow mesoarial fold of peritoneum from that part of the dorsal wall of the abdominal cavity which corresponds with the ventral face of the air-bladder. The line of attachment of the mesoarium is parallel with that of the mesentery and a little distance from it.

What may be termed the *body* of the ovary[2] is a broad and thin plate, and its inner face is covered by peritoneum. The ovarian artery enters the left ovary at its anterior internal angle, and then passes backwards along the middle of its inner face, giving off branches as it goes. The artery of the right ovary runs from behind along its dorsal edge, and then passes obliquely across its inner face forwards. The outer face of the body of the ovary gives rise to a great number of *ovigerous lamellæ* of a broadly triangular form, which are disposed transversely to the length of the organ and perpendicularly to its body (fig. 1, B, C).

[1] *Conf.* Rathke, *l.c.* p. 135.
[2] *Conf.* Rathke, *l.c.* pp. 121 & 175.

In fish which are not ready to spawn, these ovigerous lamellæ are very thick, from the number of close-set ovisacs with which they are laden, and the clefts which separate them are extremely irregular. In those in which the abdominal cavity is full of eggs, the lamellæ from which the eggs have been discharged remain as thin plates

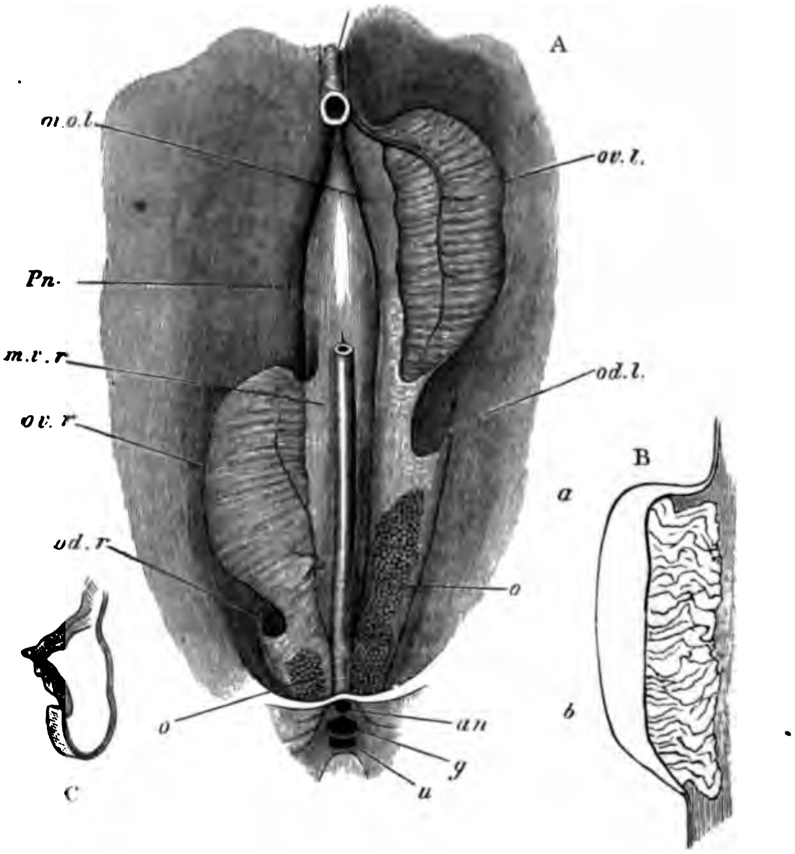


FIG. 1.—A. The genital organs of a spawning female *Osmerus eperlanus*, natural size. B. External face of the ovary. C. Transverse section.

a, œsophagus; *an*, anus; *Pn*, air-bladder; *od. r*, *od. l*, abdominal aperture of the right and left oviducts; *o*, *o*, ova filling the oviducts; *g*, external genital aperture; *m.o.r*, *m.o.l*, right and left mesoaria; *u*, urinary aperture.

separated by tolerably regular interspaces as wide as, or wider than, the thickness of each plate. The outer face of the ovary is not wholly occupied by the ovigerous lamellæ. On the contrary, the peritoneal layer of the inner face is continued over the ventral edge of the ovary, and ends at about a third or a fourth of the height of

the outer face by a well-defined margin. Hence the outer face of the ovary appears transversely laminated only above and in the middle, while below it is bounded by a smooth thin-edged band invested by peritoneum (fig. 1, B). A transverse section shows that the ovigerous lamellæ pass under this reflected band (to which their outer edges are attached) to the ventral wall of the ovary. The groove inclosed by the reflected band is thus divided into a series of interlamellar loculi (fig. 1, C).

Thus far the ovary agrees in all the essentials of its structure with that of the other Salmonidæ, and with that of all adult Ganoids except *Lepidosteus.* Even in the latter, Balfour has shown that the ovary passes through a similar condition in the embryonic state. The mesoarium, however, does not stop at the posterior end of the ovary, but, as Rathke points out, the fold of peritoneum which constitutes it is continued backwards to the oviducal aperture; while laterally it passes into the peritoneal lining of the lateral walls of the abdomen, ending in a free concave edge immediately behind and on the outer side of the posterior extremity of the ovary. It thus forms the ventral boundary of a passage which opens in front by a wide ostium into the abdominal cavity (fig. 1, *od. l*, *od. r*). As the posterior end of the right ovary lies very far behind the posterior end of the left ovary, it follows that the right ostium is equally far behind the left, and that the right passage is by so much shorter than the left. The mesentery terminates by a free posteriorly concave edge (which contains the rectal artery) just opposite the level of the posterior end of the right ovary; and, behind this free concave edge of the mesentery, the right and left passages unite in a short but wide common chamber, which opens externally in the middle line, behind the anus and in front of the urinary outlet (fig. 1, *g*).

In a Smelt ready to spawn, these passages, as well as the common chamber, are crammed full of ova; and it is obvious that, whatever their morphological nature, they are, in a physiological sense, oviducts comparable to Fallopian tubes.

But every one who is familiar with the anatomy of the female reproductive organs of the Ganoids, will at once perceive that these passages are the homologues of the oviducts of *Acipenser*, *Polyodon*, *Polypterus*, and *Amia* (fig. 2, p. 568). Neither in structure, nor in their essential anatomical relations, is there any difference between them. It is true that, in the Ganoids in question, the oviducts communicate with the renal ducts, and that the excretory aperture is common to the urinary and the genital apparatus, while in the Smelt there is no such communication and the oviducal and renal apertures

are separate. But, among the *Sturiones* and in *Lepidosteus*, the renal are much wider than the genital ducts, and the communication between the two is effected far in front of the external aperture, while in *Polypterus* and *Amia* the oviducts are much wider than the ureters and the communication takes place near the external aperture. Thus the arrangement in *Osmerus* represents simply the

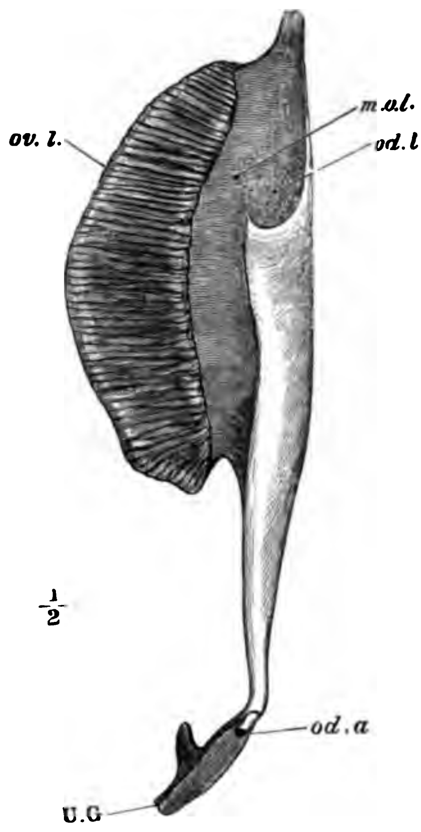


FIG. 2.--The left ovary and oviduct of *Amia calva*, half natural size.

ov. l, left ovary; *m.o. l*, left mesoarium; *od. l*, left oviduct; *od. a*, opening of the oviduct into the "bladder."

third term of a series of modifications, tending towards the separation of the ureteric from the oviducal ducts, two terms of which are presented by the Ganoids. And it follows that the arrangement of the parts which obtains in the ordinary Salmonidæ is a fourth term in the same series; that is to say, the abortion of the oviducts, commenced in *Osmerus*, is completed in *Salmo*; and all that remains of the primitive arrangement is the fold described by Rathke and the

so-called "abdominal pore," which, it will be observed, is the homologue of half of the urinogenital opening of the Ganoids, and has nothing to do with the "abdominal pores" of these fish and of the Selachians.

As is well known, *Lepidosteus* presents an example of a Ganoid with oviducts like those of the higher Teleostei; in *Osmerus*, on the other hand, we have a Teleostean with oviducts like those of the ordinary Ganoidei. It is tolerably obvious, therefore, that the characters of the female reproductive organs can lend no support to any attempt to draw a sharp line of demarcation between the Ganoids and the Teleosteans.

Boas [1] has recently conclusively shown that the same is true of the supposed distinctive character afforded by the conus arteriosus; and it has long been admitted that the spiral valve which has been described in the intestine of *Chirocentrus* [2] is the homologue of that which exists in all the Ganoids, though greatly reduced in *Lepidosteus*. Indeed I am inclined to believe that the circular valve which separates the colon from the rectum in the Smelt is merely a last remainder of the spiral valve. Thus, among the supposed absolute distinctions between the Ganoids and the Teleostei, only the peculiarities of the brain, and especially the so-called chiasma of the optic nerves, remain for consideration. My lamented friend Mr. Balfour, in the last of his many valuable labours, proved conclusively that the brain of *Lepidosteus* is, both in structure and development, a Teleostean brain. But it is singular that no one, so far as I know, has insisted upon the fact, not only that the Teleostean brain is essentially similar to that of the Ganoids, but that it is exactly in those respects in which the Ganoids and Teleostei agree in cerebral structure that they differ most markedly from the Plagiostomi and the Chimæroidei.

In a communication read before this Society some years ago,[3] I pointed out that the parts of the brain termed cerebral hemispheres in the Selachians arise in a very peculiar manner, the anterior cerebral vesicle becoming subdivided by a median anterior partition,

[1] "Ueber den Conus arteriosus bei *Butirinus* und bei anderen Knochenfischen," Morphol. Jahrbuch, vi. 4, 1880.

[2] Doubts have been thrown on the existence of this structure in *Chirocentrus*; so that the matter needs reinvestigation. [By the kindness of Dr. Day I have been enabled to examine a small specimen of *Chirocentrus dorab*; and I find it to possess just such an intestinal valve as that figured by Valenciennes. Whether it is truly "spiral" in its arrangement, or not, can only be determined by the examination of a larger specimen.—T. H. H., July 1, 1883.]

[3] "On *Ceratodus forsteri*," Proc. Zool. Soc. January 4, 1876.

and the walls of the two ventricular cavities thus formed becoming greatly thickened. The lateral walls of the undivided part of the anterior vesicle also become thickened to form the optic thalami; but these give rise to no lobular outgrowths from their upper edges.[1]

In the Ganoids the anterior cerebral vesicle undergoes a totally different series of modifications, inasmuch as no median septum is developed and no lateral ventricles are produced. In the *Sturiones* the thick lateral walls of the anterior cerebral vesicle give rise to no distinct superior lobes. In *Lepidosteus*, however, as Balfour has shown, such solid lobular bodies, or *epithalami*, are developed, and, giving rise to a thickened decurved overlapping rim from their outer faces, become exactly similar to the so-called "cerebral hemispheres" of the Teleosteans. In all the Teleosteans, in fact, the bodies called "cerebral hemispheres" are not the exact equivalents of the structures so named either in the higher Vertebrata or in the Selachians, but are *epithalami*, just as in the Ganoids. Thus, in cerebral structure, as in other respects, the Ganoids and the Teleosteans are as closely related to one another as they are different from the Selachians.

With respect to the chiasma of the optic nerves, the exact nature of that structure has not yet been properly elucidated either in the Selachians or in the Ganoids. But, whatever may come of such an investigation, the establishment of the existence of a true chiasma in the Ganoids, and of its absence in Teleosteans, can have but little bearing on the question of their affinities, since Wiedersheim has shown that a simple decussation of the fibres of the optic nerves, as in ordinary Teleosteans, takes place in many Lizards.

I am no great believer in the permanent value of sharply drawn distinctions of any kind in zoology; but, assuredly, if there is any such distinction to be drawn on the basis of our present knowledge among the higher fishes, it is between the Ganoids and the Plagiostomes, and not between the Ganoids and the Teleosteans.

At page 373 of Dr. Günther's work 'On the Study of Fishes, published in 1880, he affirms broadly and without the least qualification that, though "we find not a few analogous forms in both series" [namely the Ganoidei and the Teleostei], yet "there is no direct genetic relation between those fishes, as some naturalists were inclined to believe." I imagine that I am included among the naturalists thus summarily disposed of, since, in 1876, I expressed the opinion that "in *Amia* there is an even closer approximation between the Ganoids and the Teleosteans than can at present be shown to exist between any Ganoids and the Dipnoi; while the differences between the

[1] See Balfour, 'Development of the Elasmobranchs.'

Dipnoi and the Chimæroidei and between the Chimæroidei and the Plagiostomi respectively are not less than those between the Ganoids and the Dipnoi"[1]; and I objected on these grounds to the adoption of the group of "Palæichthyes" proposed by Dr. Günther.

When objections are ignored without being refuted, or even discussed, I suppose that the best way is to emphasize them afresh; and I do this, on the present occasion, by expressing my conviction, first, that there are no two large groups of animals for which the evidence of a "direct genetic connexion" is better than in the case of the Ganoids and the Teleosteans; and, secondly, that the proposal to separate the Elasmobranchii, Ganoidei, and Dipnoi of Müller into a group apart from, and equivalent to, the Teleostei appears to me to be inconsistent with the plainest anatomical relations of these fishes.

[1] "On *Ceratodus forsteri*," P. Z. S. 1876.

XXXIV

OYSTERS AND THE OYSTER QUESTION

The English Illustrated Magazine, 1883–1884, *pp.* 47–55, 112–121. (*A lecture delivered at the Royal Institution, Friday, May* 11*th*, 1883, *with additions*.)

IF the conversation which takes place at dinner-tables, especially in that incipient stage of content which follows upon the bad quarter of an hour of waiting, is a fair test of the public interest in any topic, I imagine that the great oyster question may be said to be that about which the general mind is most exercised.

It is a matter which concerns me personally because, since it is known that I hold the office of Inspector of Fisheries, I am almost sure to be attacked, before I have had time to squeeze my lemon, with inquiries why oysters are so dear, and why I do not do something to make them cheaper, just as if I were the minister for molluscous affairs and responsible for their going wrong. So, perhaps, I may be permitted to say publicly, once and for all, that, at present, I have nothing to do with sea fisheries, and therefore that oysters are out of my province. Twenty years ago, however, when I was a Sea Fisheries Commissioner, they were very much in it, on their practical side; while it must be near double that time since they first began to interest me from a scientific point of view. And I have thought it might be interesting to many if I tried to put together into brief compass, the pith and substance of as much as I have been able to learn in the course of my zoological life, about the facts upon which any rational discussion of the oyster question must be based.

And, first, as to the structure and ways of the oyster, of which we must obtain some knowledge if the discussion is to have a sound basis. I suppose that when the sapid and slippery morsel—which is and is gone, like a flash of gustatory summer lightning—glides along

the palate, few people imagine that they are swallowing a piece of machinery (and going machinery too) greatly more complicated than a watch. But so it is; the oyster possesses representatives of all the most important organs of the higher animals, and is endowed with corresponding functions. The "loves of the oyster" may be mythical, and we may even be sceptical as to its parental tenderness; but no parent can take greater care of its young. And though the oyster seems the type of dull animal vegetation in its adult condition, it passes through a vagabond, if not a stormy youth, between the time in which it is sheltered by the parental roof, and that in which it "ranges" itself as a grave and sedentary member of the oyster community.

Most people are familiar with the appearance of a live oyster, as it may be seen any day in a fishmonger's shop (Fig. 1). It has a shell composed of two pieces or *valves*, the one of which is thick and has a convex outer surface, while the other is thinner and flattened. The contour of each valve is irregularly oval, with a small end, which usually presents a triangular prominence known as the *umbo* or beak (*um.*), and which answers to the back or dorsal region of the animal. When this is turned upwards, the opposite or ventral margin is seen to be evenly curved, and to be gradually continued into the curved line of the front margin (*ant.*), while the hinder margin (*post.*) is usually straighter. By attention to these characters, the right valve can always be distinguished from the left; but, in the great majority of cases, it is more easily known because it is the flat valve. If the oyster is fixed, it is the convex valve which is attached; and free oysters naturally lie on this valve, inasmuch as the other is the lighter, and the more easily raised by the mechanism which will be presently described.

The exterior of the shell is rough and usually of a brownish-green colour. It is marked by lines, which run approximately parallel with the contour of the shell, around a common centre placed at the summit of the umbo, and indicate the successive layers by the apposition of which the shell has been deposited upon the skin of the animal. The inner face of each valve has the well-known white and opaline or iridescent aspect which appertains to nacre or mother of pearl, except the flattened or concave surfaces of the umbones, which are marked by parallel lines answering to the lines of growth on the exterior. At the bases of the umbones, the valves are joined together, along a short transverse line, in a sort of hinge by a band of dark-brown elastic substance, the *ligament* (*l.*), which, in the middle of the hinge, forms a thicker cushion. About the centre of the inner

face of each valve there is a large well-defined rounded depression like a scar, which marks the place of attachment of a strong and important muscle.

Each valve is sometimes solid throughout, but in old oysters, and especially in those that live in deep water, the substance of the valves, and more particularly of the thick convex left valve, contains wide cavities, separated only by thin layers of nacreous substance, which are full of sea-water.

In structure, the nacre, or mother of pearl, is very dense, hard, and finely laminated; but the superficial outer layer is made up of small polygonal prisms, and is somewhat friable. Each of these substances, the nacreous and the prismatic, consists of layers of organic matter impregnated with salts of lime.

If the oyster has been left at peace for some time in its native sea-water, the edges of the valves, beyond the hinge, will be seen to be separated by a chink which is wider opposite the umbones. But, upon the least disturbance, the chink is closed and the shut valves cannot be thrust asunder, without the expenditure of an amount of force which usually breaks them.

An expert oyster opener, however, mindful of the maxim, *arte non vi*, gets them apart with the utmost ease. A strong flat-bladed knife is introduced between the margins of the valves, and the knife being kept close to the inner face of one of them, is swept round the region of the muscular impression. If the operation is properly performed, the shell at once gapes widely; and it will now be found that, if the valve which has sprung up is pressed down, it immediately returns to its former position. The shell that, before, could hardly be forced open, now will not keep shut. The reason of this becomes apparent if the soft body, the edible part of the oyster, which lies within the shell is carefully cleaned out so that the interior of the valves can be seen. On looking towards the hinge, the thick elastic cushion formed by the middle of the ligament, will be found to be compressed when the valves are brought together, and, when the external pressure is removed, its elastic reaction suffices to thrust them apart. In fact, it is like the spring of a door, arranged in such a manner as to keep the door ajar. While the oyster is alive, the great muscle already mentioned, which is called the *adductor* (Fig. 1, *add.*), the ends of which are attached to the two scars on the inner face of the valves, is always ready to overcome the elasticity of the ligament and close the valves, when need arises. And what the judicious oyster opener does is to cut this muscle close to one or other of its attachments. Thus the force by which the valves are made to gape is elasticity of a

purely mechanical character, and is as active in the dead as in the living oyster; while that by which the valves are closed is the contractility which inheres only in living muscle. Hence a dead oyster is readily known by its persistent gaping.

We shall see that a certain amount of separation of the valves is necessary for the discharge of all the functions of the living oyster. Hence, it is of advantage to the animal that this condition should be assumed and maintained without any muscular exertion; while intruders and enemies can be shut out, or at any rate sharply pinched, at any moment, by calling the adductor into action.

If one valve is removed very carefully, so as not to injure the soft body within, the form of the latter is seen to have a general

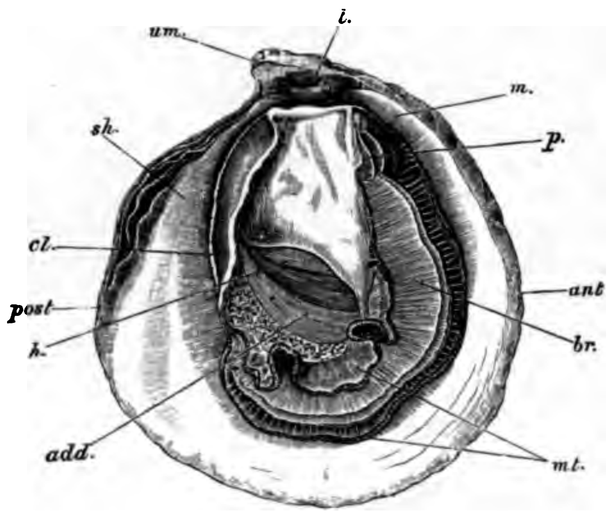


FIG. 1.—An Oyster with the right valve of the shell removed. Natural Size.
sh. shell; *um*, umbo; *l.* ligament; *m.* mouth; *p.* palps; *br.* branchiæ; *mt.* mantle; *add.* adductor muscle; *h.* heart; *cl.* cloaca; *ant.* anterior; *post.* posterior side.

correspondence with that of the interior of the shell. It is therefore flattened from side to side, with the left side convex and the right flattened (Fig. 1). Its contour is oval, with the long axis perpendicular to the middle of the hinge; and there is a short dorsal side which answers to the latter, and is excavated in the middle, in correspondence with the convex ventral face of the cushion of the ligament. The dorsal half of the anterior edge of the body is convex, that of the posterior edge is nearly straight, or even slightly excavated, while the ventral margin continues back the curve of the anterior edge. The cut end of the thick adductor muscle is a

conspicuous object, and corresponds in shape with the adductor impression on the shell. That is to say, it has the form of a half oval, the straight side of which looks dorsally and a little forward. The upper and anterior portion of the muscle is darker than the rest and sharply defined from it (Fig. 1, *add.*).

Just above the straight side of the muscle, a dark patch indicates the place of the heart, which may be seen pulsating in the chamber or *pericardium*, which contains it (Fig. 1, *h.*). Above this the surface of the body is covered by a smooth and delicate skin or integument, through which, in the breeding season, the reticulated whitish tubes of the reproductive gland shine.

The chief part of the body of the oyster, which for want of a better name may be termed the *trunk*, is a somewhat pyriform mass which extends from the ventral contour of the adductor to the posterior half of the dorsal region, and lies much more in the posterior than in the anterior half of the body (Fig. 2 (A)).

The rest of the body of the mollusk is chiefly formed by two broad folds of the integument which are given off from the lateral margins of the trunk on each side; extend backwards, forwards, and downwards; and, closely applied to the inner surfaces of the valves, end by thickened free margins, which have two rows, an inner and an outer, of close-set papillæ. These free folds of the integument are called the *lobes of the mantle* (Fig. 2 (B), *r. mt.*, *l.mt*). Their surfaces are attached by a series of delicate muscular fibres to the inner surface of the shell, at some distance from its margin and from their own free edges; and, in the living state, the fringe, beyond the line of attachment, extends to the edges of the gape and plays the part of a sensory apparatus. The margins of the mantle lobes pass into one another above, at the anterior and posterior ends of the dorsal integument respectively, so that the cleft between them does not extend on to the dorsal surface. The lobes are much deeper in front and below than behind; hence the cavity which they inclose is correspondingly deeper and shallower in the respective regions. If one lobe is cut through, immediately beneath the anterior end of the dorsal integument, and turned back, it is seen to bound a wide space which extends back a long way, in fact nearly to the posterior side of the trunk. This is the *vestibule* (Fig. 2 (A), *vb.*), and the dorsal integument which covers it is the anterior hood or *cucullus* (Fig. 2 (A), *c.*). Projecting into this is seen a sort of cone which at its upper and front end bears the wide slit-like mouth, bounded by broad lips, one above and one below. The angles of these lips are produced, like an upper and lower moustache, into two broad triangular flaps, the

so-called *labial palps* (Fig. 2 (A), *p.*). Below these, the mantle lobes, throughout their anterior and ventral regions, include a wide space termed *infrabranchial* (Fig. 2 (B), *in.br.ch.*), because the four plates which constitute the gills or *branchiæ*, and are commonly called the "beard," project into it and form its roof. Each of these plates or *lamellæ* is V-shaped in tranverse section (Fig. 2 (B)). The adjacent upper ends of the four V's (VVVV) are united together, while the outer ends of the right and left V's respectively are attached to the corresponding lobes of the mantle. Hence the gill plates hang down, like so many elongated Gothic sickle-shaped pendants, from the roof of the branchial cavity, which is formed by their conjoined edges. On the posterior side, the cavity inclosed between the pallial lobes is deep below, but rapidly becomes shallower above, where the lobes are narrowed to mere bands. The two bands pass into one another at the posterior end of the dorsal integument—and form a rudimentary posterior hood, the *velamen* (Fig. 1 (A), *ve.*), which is very large in many other Lamellibranchs. The intestine projects beneath the integument as it runs obliquely downwards, over the posterior face of the adductor, to end in the short but prominent tubular vent. The posterior interpallial space into which this opens answers to the *cloacal chamber* of other Lamellibranchs (Fig. 1 and Fig. 2 (A), *cl.*). It is continued forwards, between the trunk and the dorsal faces of the gills, into a long *suprabranchial chamber* (Fig. 2 (A), *su.br.ch.*), which extends forwards and upwards, in front of the trunk, as far as the anterior and superior ends of the gills. For their anterior third, the dorsal edges of all the gills become attached to the front face of the trunk. The suprabranchial chamber thus becomes subdivided into four passages, which end blindly in front. The *intralamellar* cavities, which are inclosed by each V-shaped branchial plate, communicate, either indirectly through these passages, or directly, with the suprabranchial chamber, and this widens behind into the cloacal chamber, which opens freely on to the exterior upon the posterior side of the body. But the suprabranchial chamber, its passages, and the intralamellar cavities, would be completely shut off from the infrabranchial chamber by the walls of the gill plates, were it not that these walls are perforated, like a sieve, by multitudes of very narrow parallel slits.

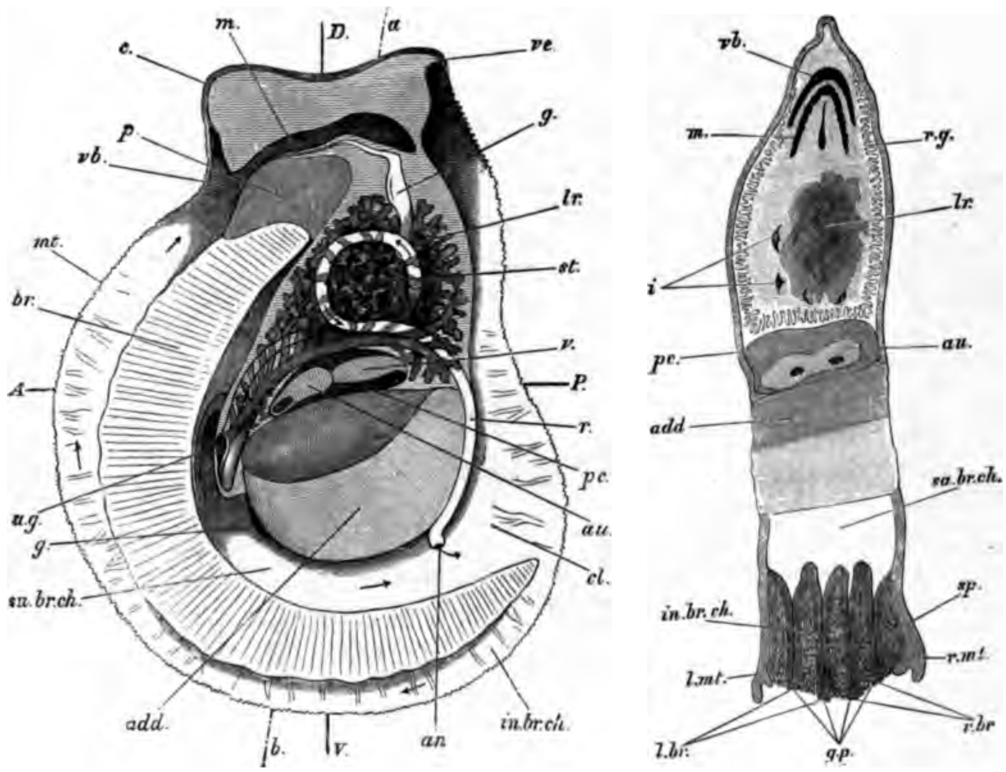
The mouth of the oyster leads into a wide gullet, which passes back for a short distance, and then dilates into a spacious stomach, the lower and anterior end of which is continued into the long conical first part of the intestine, which passes downwards in front of the adductor, closely applied to its anterior contour. The next portion of

the intestine then bends sharply upon itself and turns forwards parallel with the first part; crosses this on the right side, runs up along the back of the stomach, bends forwards and downwards, and turning back on the left side of the stomach (thus forming a completely circular loop) passes at first backwards and then downwards to the vent, the place of which has been already described (Fig. 2 (A)).

The stomach and the circular loop of the intestine are surrounded by a dark brown or greenish organ, the short branched tubules of which unite into larger tubes or ducts which open into the stomach. This organ is known as the liver—though it by no means exactly answers to the organ so called in the higher animals, but secretes the fluid which is the chief agent in digestion.

The heart (Fig. 2 (A)) lies in a spacious pericardial cavity (*pc.*) situated between the flat face of the adductor muscle, behind and below, and the mass of the digestive viscera in front and above. It consists of a large dark-coloured auricular division (*au.*), partly divided into two, which is situated below and in front and which communicates by two short tubular passages with the pear-shaped ventricle (*v.*), the long axis of which is directed upwards and backwards. Large arterial trunks are continued from the ventricle, one upwards and backwards, along the posterior moiety of the circular loop of the intestine, one forwards along the anterior moiety, one downward to the adductor. The successive contractions of the auricle and the ventricle may be readily seen in the living oyster. The blood is colourless and contains numerous colourless corpuscles. It is conveyed by the arteries to all parts of the body and thence proceeds to a large venous canal, which lies in the middle line of the anterior face of the trunk. From this it passes through the renal organs to the gills, and is thence returned by a main vessel on each side to the auricular division of the heart. The branchiæ consist of the four sickle-shaped plates already mentioned which extend, in pairs, from the palps in front and above, to near the level of the vent behind (Fig. 2 (A) *br.*). Unlike a sickle, however, it is the convex edge of each which is sharp, while the concave edge is broader. Each plate or lamella, as we have seen, is V-shaped, consisting of two *laminæ* which bound the intra-lamellar cavity, and join below to form the edge of the lamella. It can be shown that each gill plate answers to half the gill of those Lamellibranchs in which the structure of the branchia retains its primitive simplicity. Consequently the oyster has two gills and each lamella is a *hemi-branchia* made up of two *laminæ*. Of the three partitions which separate the supra-branchial passages, the right and left

represent the stems of the branchiæ, while the middle one is formed by the adherence of the edges of the inner laminæ of the two inner hemi-branchiæ to one another and to the anterior face of the trunk.



A B

FIG. 2.—(A) Dissection of an oyster from the left side.—(B) Transverse section of the same taken along the line *a. b.* in A.

D. dorsal; *V.* ventral; *A.* Anterior; *P.* posterior side; *mt.* mantle; *r. mt. l. mt.* its right and left lobes; *c.* cucullus, or anterior hood; *ve.* velamen, or posterior hood; *vb.* vestibule; *cl.* cloaca; *m.* mouth; *p.* palps; *g.* gullet; *st.* stomach; *i.* intestine; *r.* last part of the intestine; *an.* vent; *lr.* liver; *pc.* pericardium; *au.* auricle; *v.* ventricle of the heart; *br.* branchiæ; *gp.* the four lamellæ of the branchiæ, or gill-plates, of which two make up the left branchia (*l.br.*), and two the right (*r.br.*); *su.br.ch.* supra-branchial chamber: *in.br.ch.* infra-branchial chamber, the position of the "spat," or mass of eggs, being shown in the transverse section; *u.g.* urogenital aperture. The duct of the left reproductive gland is seen passing from it and ramifying over the stomach and intestine. In the transverse section, the cæca of the gland are shown forming a layer immediately beneath the integument. Those of the right gland are marked *r.g.*; *g.* position of the two principal nervous ganglia; *add.* adductor muscle.

The arrows in A indicate the course of the inflowing and outflowing currents.

Even to the naked eye the surface of a hemi-branchia appears marked with regular parallel transverse lines. And a low magnifying

power shows that these lines are the optical expression of a series of parallel foldings of the lamina. The re-entering angles of the opposite folds correspond and are united together for some distance, so that the intra-lamellar chamber, or cavity of the hemi-branchia, is divided into a series of parallel transverse tubular cavities, which are widely open above, but which narrow and apparently become closed below. The lamina itself consists of close-set parallel *branchial filaments.* Each of these filaments has the shape of a lath, about $\frac{1}{1300}$th of an inch thick, and five or six times as wide; and they are set edge-wise with their flat faces not more than $\frac{1}{5000}$th of an inch apart. At intervals, transverse bands unite these lath-shaped branchial filaments together. The outwardly turned edges of the 'laths' are closely beset with very long vibratile hair-like processes, known as *cilia;* and, during life, these work in such a fashion as to drive the water through the narrow clefts between the branchial filaments into the cavities of the tubes, whence it escapes into the supra-branchial passages and chamber and thence makes its way out by the cloacal chamber. The place of the water thus swept out of the infra-branchial chamber is, of course, made good by a corresponding flow between the pallial lobes into it. Hence, while the oyster is alive, and in its proper element, a powerful stream constantly sets in on the ventral and anterior side of the body and pours out from the cloacal opening on the posterior side. The direction of the stream is marked by the arrows in Fig. 2 (A).

It is upon the proper maintenance of this current that the life of the oyster depends. For these animals feed upon the microscopic organisms, largely consisting of diatomaceous plants, which live in the sea; and as they possess no organs for seizing such food, they are almost entirely dependent for their supply of nourishment upon the indraught caused by the cilia on the gills, and especially upon those which line the edges of the branchial plates and direct a portion of the current towards the mouth. The anterior ends of each pair of hemi-branchiæ are attached between the two palps of the side to which they belong. The applied surfaces of the palps, between which lies the commencement of the mouth-cleft, are ridged and richly ciliated, so that anything brought by the ciliary current of the gills is led directly into the oral cavity. The cilia which line this eventually drive it into the stomach. Thus the unimpeded action of the cilia of the gills is essential to the nutrition of the oyster; but it is not less necessary to its respiration, to the carrying away of the waste products of the renal and alimentary organs, and to the expulsion of the reproductive products. For all these processes depend, either on

the flow of water through the laminæ of the gills, or upon the current which sets out from the supra-branchial and cloacal chambers.

Hence the importance of tolerably clear water to oysters. If turbid water, laden with coarse sediment, enters the infra-branchial cavity, particles of mud, too large to be moved by the cilia, lodge upon the gills, and, gradually obstructing the current, interfere with the primary functions of feeding and breathing to such an extent as to injure, or even to destroy the animal.

It would be out of place here to give any account of the complicated renal organs of the oyster recently discovered and described by Dr. Hoek. But it is necessary to notice the openings by which the cavity common to them and the reproductive organs debouches. These are the small slit-like apertures (Fig. 2 (A), *ug.*), situated one on each side of the lower and front face of the trunk, which open into the supra-branchial cavity.

For the comfort of those lovers of oysters who entertain strong views upon the vivisection question, and who may be perturbed by the reflection that they not only vivisect their favourites, but swallow them alive, it may be well to remark that the nervous system of the oysters is more poorly developed than that of any of their allies among the lamellibranchiate mollusks. Only two out of the three pairs of nerve masses, or *ganglia*, which these animals ordinarily possess have been clearly made out, while, of these, the pair which is most likely to represent the sensorium of higher animals is exceedingly small. Moreover, no organs of special sense have been demonstrated. So that, if any reasoning from analogy is permissible on this subject, it is probable that the sensibility of the oyster is infinitesimally small. Of course I do not suggest that this consideration can have any value in the eyes of those who maintain that the infliction of suffering on animals for the benefit of mankind is absolutely unjustifiable. Rigorists of this class are bound to denounce the brutal deglutition of oysters, no less than the cruel crushing of fleas, and the infamous poisoning and drowning of flies and cockroaches.

Yet one other morphological observation may be permitted. The oyster, as we have seen, possesses one very large adductor muscle, but only one. Almost all other lamellibranchs (*e.g.* cockles, mussels, razor-fish) have two ; one in front, near the mouth ; and one behind, in a position which exactly answers to that of the single adductor of the oyster. The latter, therefore, is called *monomyary*, or one-muscled, while the former are *dimyary*, or two-muscled ; and a series of forms

can be selected among the sea mussels and the scallops which show the posterior adductor becoming larger and larger, while the anterior diminishes, until, in the oyster, it disappears.

During the summer and autumn months, from as early as May to as late as, or even later than, September, according to circumstances, of which the temperature and the depth of the water in which the oysters live appear to be the most influential, a certain proportion of the oysters in an oyster-bed pass into a peculiar condition, and are said by the fishermen to be "sick." In about half of these sick oysters, a whitish substance made up of innumerable very minute granules, embedded in, and held together by, a sort of slime, collects in the infra-branchial chamber, filling up the interspaces between the mouth and the gills, and between the gill plates themselves, and even occupying the vestibular cavity so completely that it is difficult to understand how the processes of breathing and feeding can be carried on (Fig. 2 (B)).

This granular slime is what is known as "white spat," and the granules are the eggs of the oyster. By degrees, the granules become more or less coloured ; and the mass, acquiring a brownish hue, is termed "black spat." This change depends on the development of the young, which acquire a certain degree of coloration, within the eggs. At the end of a period, the length of which varies with the temperature of the water and other conditions, but appears rarely to exceed a fortnight, the mass of black spat breaks up, and the young, hatched out of the eggs, leave the mantle cavity of the parent in which they have been thus incubated. They become diffused through the water, and swarm in vast multitudes at the surface of the sea.

A single full-grown oyster produces, on the average, about a million of these free-swimming young or *larvæ*. If a glass vessel is filled from the stratum of surface water, in which the larvæ swim, and held up to the light, it will appear full of minute particles—only $\frac{1}{150}$th of an inch long, and therefore just visible to the naked eye—which are in active motion. An ordinary hand magnifier is sufficient to show that these minute organisms have very much the aspect of the *Rotifera*, or "wheel animalcules," so common in fresh water. They have a glassy transparency, and are colourless, except for one or more dark brown patches ; while, at one end, there is a disk, like the "wheel" of the Rotifers, the margins of which are apparently in rapid motion, and which serve as the organs of propulsion. When this propeller is moderately active, the larvæ dance up and down in the water, with the

disk uppermost; but when the action is more rapid, they swim horizontally with the disk forward.

How long the larval oysters remain in this locomotive state, under natural conditions, is unknown, but they may certainly retain their activity for a week, as I have kept them myself in a bottle of sea water, which was neither changed nor aerated, for that period. But sooner or later, they settle down, fix themselves by one side to any solid body, and rapidly take on the characters of minute oysters, which have the appearance of flattened disks, $\frac{1}{20}$th of an inch, more or less, in diameter; they are therefore perfectly visible, as white dots, on the surface of the substance to which they adhere. In this condition, the name of "spat" is also applied to them. The locomotive larvæ being practically invisible in the sea, this spat appears to be as it were precipitated out of the water; and since great quantities appear at once, the oyster fishermen speak of a "fall" of spat.

It is important to observe, that when oyster fishermen say that there has been no "fall" of spat in a given season, all that is really implied is that the young fixed oysters have not made their appearance. The fact of the absence of a "fall of spat" does not justify the conclusion that the oysters have not bred as usual. It is quite possible, that just as many eggs have been deposited in the branchial cavity, and that just as many larvæ have been set free as in other years; but that the larvæ have been destroyed by those changes of temperature to which they are so sensitive, or by other causes. But, of course, it is also quite possible that the oysters have been really barren; or that although the eggs have reached the mantle cavity, the larvæ have not hatched out. Oyster eggs, no less than hens' eggs may be addled.

It is obviously useless to speculate upon the causes of a "failure of spat," until, by the examination of samples of oysters from time to time, and by sweeping the superjacent water with a fine towing net, the exact nature of the particular case of failure has been ascertained. There is much reason to believe that the fertility of oysters, preserved in parks, is greatly diminished, although the oysters themselves may be improved in fatness and quality by the process, and that this is especially the case when the water in which they are preserved has a low degree of salinity; and it is very desirable to ascertain the nature of the modifications effected in the structure and functions of the reproductive apparatus of the oyster under these circumstances.

It is unfortunate that the same word "spat" should be applied to things so different in their nature, as the eggs and unhatched young of the oyster, contained within the mantle cavity, on the one hand,

and the young fixed oysters, on the other; while there is no familiar name for the very important stage of development which lies between these two. "Brood," "fry," and "spat" would be very convenient names for the three stages, if "brood" were not already in use for the smallest of the young fixed oysters. Perhaps the most convenient course will be to use "fry" for the eggs or embryos which are contained within the mantle cavity of the parent; "larvæ" for the locomotive stage; and "spat" for the final condition.

In order to become spat, the larva appears invariably to fix itself by one side (almost always the left); and, if the surface is favourable, the extent of the surface of adhesion becomes very considerable, and the oyster is fixed throughout life. But, if the surface of adhesion is small, the oyster, as it increases in size, readily becomes detached and lies free, though motionless, on the bottom.

The young oysters grow very rapidly. In five or six months, they attain the size of a threepenny piece; and, by the time they are a twelvemonth old, they may reach an inch or more in diameter. The rate of growth varies with the breed of oyster, and with the conditions to which it is exposed; but it is a roughly accurate and convenient way of putting the matter to say, that, at two years, the oyster measures two inches across, and at three years, three inches. After this, which may be regarded as the adult age, the growth is much slower, and the shell increases in thickness, much more than in circumference.

The natural term of the oyster's life is not known, but there is reason to believe that it may extend to twenty years or more. An excellent authority, Professor Möbius, is of opinion that most of the adult Schleswig oysters are from seven to ten years old, and that, though oysters over twenty years of age are rare, he has met with occasional specimens which had attained between twenty-five and thirty years.

Oysters breed long before they are full grown, very probably in the first year of their age, certainly in the second. Their productivity appears to reach its maximum at five or six years, and afterwards to decline; but much further observation is needed before any definite rules can be laid down on this subject.

These are the most important obvious phenomena presented by the reproductive processes of the oyster.[1] We must now consider

[1] It must be remembered that the account here given holds good only of the *Ostrea edulis* of England and Northern Europe. In the Portuguese Oyster (*O. angulata*) and the American Oyster (*O. virginiana*) the eggs are set free at once, and are not incubated in the mantle cavity of the parents.

them a little more in detail, and under those aspects which are hidden from ordinary observation.

The oyster, like other animals, takes its origin in an egg, or *ovum*, a minute, relatively structureless, protoplasmic spheroidal body, about $\frac{1}{250}$th of an inch in diameter, by a long series of developmental changes which take place in that ovum after it has united with another living particle of extremely minute size, the *spermatozoon*, and in consequence of the fertilisation effected by that union, just as the ovule of a plant develops in consequence of the influence of the pollen upon it. And the first problem is, Where are these ova and spermatozoa formed? Does each oyster produce both, or are they formed in distinct oysters? This is, in fact, the vexed question of the sexes of the oyster, which has been the subject of so much discussion, and for which the answer is gradually shaping itself, thanks mainly to the recent labours of Möbius and Hoek.

I have already stated that if the surface of the trunk of a full grown oyster is examined carefully with a lens, or even without one, a curious ramified and more or less reticulated whitish marking, which is very obvious in the breeding season, is observable beneath the thin integument. By appropriate methods of investigation it is easily determined that this marking is produced by the ramifications of a tubular organ,—the *reproductive gland*—the trunk of which debouches into a cavity common to it and the renal organs, which again, it will be recollected, communicates by a narrow slit with the supra-branchial chamber (Fig. 2 (A), *ug.*). The trunk of the gland, on each side, passes upwards and backwards, in front of and above the adductor and muscle, and gives off a multitude of branches, some of which cross the middle line and become inextricably united with those of the other side, while others form a network beneath the skin which covers the stomach and the liver. From this network, blind offshoots are given off perpendicularly inwards, and extend for a variable depth into the interior of the body. The whole extent of the walls of the tubes of this reproductive gland is lined by nucleated cells, and it is by the metamorphoses of these cells that the ova, on the one hand, and the spermatozoa, on the other, are produced.

During the breeding season, an examination of the adult oysters on an oyster bed shows that the number of individuals the reproductive glands of which contain hardly anything but ova is about equal to that of the individuals in which the reproductive gland contains hardly anything but spermatozoa. I say "hardly anything" because competent observers have affirmed, that careful search will always reveal a few spermatozoa, in the former, and a few ova, in the

latter Whether this be so or not, there can be no doubt that, practically, oysters, while actually breeding, are either males or females.

When the ova or spermatozoa are ripe, they flow out of the reproductive gland into the surrounding water. The spermatozoa are carried away by the exhalent currents of the oyster in which they are developed, and are doubtless drawn in by the inhalent currents of adjacent oysters, the eggs of which they fertilise. And, as the eggs already exhibit the first of that series of changes which lead to the formation of the larva, when they leave the reproductive gland, it would appear that they must undergo fertilisation while still within that organ.

The eggs which pass into the supra-branchial chamber must also be driven out by the exhalent current; but it would seem that, when they reach the hinder edge of the branchial partition, they come within the influence of the inhalent current and are thereby swept back into the infra-branchial chamber. Here they accumulate, and becoming embedded in a viscid albuminous matter, secreted by the parent, constitute the "white" fry (Fig. 2 (B)).

From the nature of the case, this account of what takes place is not the result of direct observation; but it seems to be by far the most probable explanation of the facts which can be observed. In an oyster which contains white fry, in fact, the reproductive gland is flaccid, and contains nothing, or hardly anything, but a few unexpelled ova.

The case is different, however, with oysters the eggs of which have been laid so long that they have passed into the condition of "black spat." Here many, or, as I have recently found in one case, the great majority, of the tubes of the gland contain developing spermatozoa, while only a few exhibit ova. And Dr. Hoek has recently made the important observation that, if an oyster which contains fry is kept for a fortnight in an aquarium by itself and then examined, the reproductive organ will be found no longer to contain ova, but abundant developing and fully formed spermatozoa.

After producing eggs, in fact, the female oyster changes its sex and becomes male.

The conclusion, first advocated by M. Davaine many years ago, that the same individual oyster is alternately male and female, is therefore unquestionably correct. What has yet to be made out is the period of recurrence of this extraordinary alternation of sexes. Do oysters change their sexes once or more than once in a season?

Until this point is ascertained, all calculations as to the proportionate number of oysters which breed during a season, based on the observation of the proportion of those which at any given time contain fry, are obviously unsafe. If, for example, the alternation took place once a month, not more than half the oysters might at any time contain fry, and yet, in four months, every oyster might have spatted twice.

In the case of the Portuguese and the American oysters, in which both the reproductive products pass at once into the water and no incubation takes place, artificial fecundation is easily effected. The embryos develop normally, pass through their changes within the egg, and their locomotive stage, into the condition of fixed oysters rapidly, when confined in properly arranged aquaria. It is probable, therefore, that artificial breeding will sooner or later be practised on a great scale with these oysters. In the case of our own oysters, artificial propagation by the methods practised in the case of the Portuguese and American forms, which involve the destruction of both parents, is obviously out of the question, unless some substitute can be found for the process of incubation, during which it is probable that the young oysters receive, not merely shelter but nourishment, from the parent. But a careful study of the conditions under which our oysters breed freely, will no doubt enable oyster cultivators to imitate these conditions—and to place their breeding stock under circumstances in which hurtful influences shall be excluded, while the larvæ are prevented from wandering too far and facilities are afforded for their attachment. The oyster grounds at the mouth of the Scheldt, of which a very interesting account was given by Dr. Hubrecht at one of the conferences of the International Fishery Exhibition [1] seem to be in a fair way of realising these conditions.

It has been seen that the young animal which is hatched out of the egg of the oyster is extremely unlike the adult, and it will be worth while to consider its character more closely than we have hitherto done.

Under a torerably high magnifying power the body is observed to be inclosed in a transparent but rather thick shell, composed, as in the parent, of two valves united by a straight hinge (Fig. 3 A. *h.*). But these valves are symmetrical and similar in size and shape, so that the shell resembles that of a cockle more than it does that of an adult oyster. In the adult, the shell is composed of two substances of different character, the outer brownish, with a friable prismatic

[1] Papers of the Conferences. "Oyster Culture and Oyster Fisheries in the Netherlands," by Professor Hubrecht.

structure, the inner dense and nacreous. In the larva, there is no such distinction, and the whole shell consists of a glassy substance devoid of any definite structure.

The hinge line answers, as in the adult, to the dorsal side of the body. On the opposite, or ventral side, the wide mouth (*m.*) and the minute vent (*an.*) are seen at no great distance from one another. Projecting from the front part of the aperture of the shell there is a sort of outgrowth of the integument of what we may call the back of the neck, into a large oval thick-rimmed disk termed the *velum* (*v*), the middle of which presents a more or less marked convex prominence. The rim of the disk is lined with long vibratile cilia, and it is the lashing of these cilia which propels the animal, and, in the absence of gills, probably subserves respiration. The funnel-shaped mouth has no palps; it leads into a wide gullet and this into a capacious stomach. A sac-like process of the stomach on each side (*r.l.*, *l.l.*) represents the "liver." The narrow intestine is already partially coiled on itself, and this is the only departure from perfect bilateral symmetry in the whole body of the animal. The alimentary canal is lined throughout with ciliated cells, and the vibration of these cilia is the means by which the minute bodies which serve the larva for food are drawn into the digestive cavity.

There are two pairs of delicate longitudinal muscles (*r.s.*, *r.i.*) which are competent to draw back the ciliated velum into the cavity of the shell, when the animal at once sinks. The complete closure of the valves is effected, as in the adult, by an adductor muscle, the fibres of which pass from one valve to the other. (Fig. 3 *a. add.*) But it is a very curious circumstance that this adductor muscle is not the same as that which exists in the adult. It lies, in fact, in the fore part of the body, and on the dorsal side of the alimentary canal. The great muscle of the adult, on the other hand, lies on the ventral side of the alimentary canal and in the hinder part of the body. And as the muscles, respectively, lie on opposite sides of the alimentary canal, that of the adult cannot be that of the larva which has merely shifted its position; for, in order to get from one side of the alimentary canal to the other, it must needs cut through that organ. But, as in the adult, no adductor muscle is discoverable in the position occupied by that of the larva, or anywhere on the dorsal side of the alimentary canal; while, on the other hand, there is no trace of any adductor on the ventral side, in the larva—it follows that the dorsal or anterior adductor of the larva must vanish in the course of development, and that a new ventral or posterior adductor must be

developed to play the same part and replace the original muscle functionally, though not morphologically.[1]

This substitution is the more interesting, since it tends to the same conclusion as that towards which all the special peculiarities of the oyster lead us; namely, that, so far from being a low or primitive form of the group of lamellibranchiate mollusks to which it belongs, it is in reality the extreme term of one of the two lines of modification which are observable in that group. The *Trigoniæ*, the arks, the cockles, the freshwater mussels, and their allies, constitute

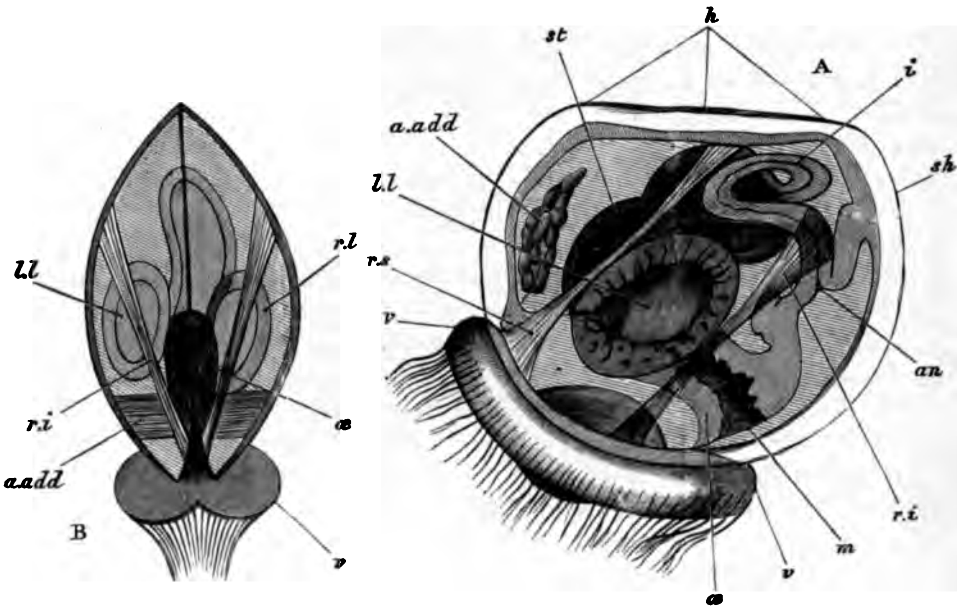


FIG. 3.—The Larva of the Oyster.

A; side view. B; front view. *v.* velum with its long cilia; *æ.* œsophagus or gullet; *st.* stomach; *r.l. l.l.* right and left lobes of the 'liver;' *i.* intestine; *an.* vent; *a. add.* anterior adductor muscle which alone exists in the larva; *r.s,r.i.* superior and inferior muscles which retract the velum into the shell, *sh.*; *h.* hinge of the shell.

the central and typical group of these mollusks. They possess two sub-equal adductors, a large foot, and a body which is neither very deep nor very long. From these, the series of the boring bivalves exhibits a gradual elongation of the body, ending in the ship-worm (*Teredo*) as its extreme term. While, on the other hand, in the sea mussels, the *Aviculæ*, and the scallops, we have a series of forms

[1] The larva of the cockle has at first, like the oyster larva, only one adductor, which answers to the anterior of the two adductors which the cockle possesses in the adult state.

which, by the constant shortening of the length and increase of the depth of the body, the reduction of the foot, the diminution of the anterior of the two adductors, and the increase of the posterior, until the latter becomes very large and the former disappears, end in the oyster.

And this conclusion that the oysters are highly specialised Lamellibranchs, agrees very well with what is known of the geological history of this group, the oldest known forms of which are all dimyary, while the monomyary oysters appear only later.

When the free larva of the oyster settles down into the fixed state, the left lobe of the mantle stretches beyond its valve and applying itself to the surface of the stone or shell, to which the valve is to adhere, secretes shelly matter, which serves to cement the valve to its support. As the animal grows, the mantle deposits new layers of shell over its whole surface, so that the larval shell valves become separated from the mantle by the new layers which crop out beyond their margins and acquire the characteristic prismatic and nacreous structure. The summits of the outer faces of the umbones thus correspond with the places of the larval valves, which soon cease to be discernible. After a time, the body bocomes convex on the left side and flat on the right; the successively added new layers of shell mould themselves upon it; and the animal acquires the asymmetry characteristic of the adult.

Oysters are gregarious, in consequence of the vast multitude of locomotive larvæ which are set free simultaneously; and which, being subjected to the same influences, tend to settle about the same time in the area to which the swarm drifts. Millions of oysters are thus aggregated together over stretches of the bottom of the sea, at depths of from one or two, to twenty or more, fathoms, and constitute what are known as oyster beds.

Although oysters live and grow well enough in estuaries, in which the salinity of the water undergoes large variations, according to the state of the tide and the volume of fresh water that is poured in, yet they do not flourish permanently and breed freely in water with less than 3 per cent. of saline constituents. Thus the Baltic is, at present, unfit for their support; and the east coast of Schleswig, washed by its brackish waters, is devoid of oysters, while certain parts of the west coast are famous for their oyster beds. Gravel, stones, and dead shells—commonly known as "cultch"—form the most favourable bottom, as they facilitate the attachment of the young. Disturbed

muddy bottoms, on the other hand, are fatal, for reasons which have already been given. But it is a curious fact, that even where a large extent of sea-bottom presents apparently the same conditions, oyster beds occur in some localities and not in others.

The struggle for existence is as intense in the case of the passive oyster as in that of the most active of animals. Oyster competes against oyster for the common store of food suspended in the water, and for the dissolved carbonate of lime out of which the shell must be made. Innumerable other animals, sponges, corallines, polypes, tunicates, other bivalve mollusks, especially mussels and cockles, live in the same way and abound on oyster beds, often attached to the shells of the oysters. Prof. Möbius counted as many as 221 distinct animals of various species on one oyster shell. All these compete with the oyster for food, while, on the other hand, they may occasionally supply food to the oyster in the shape of débris, and, perhaps, of their eggs and microscopic larvæ.

From birth onwards oysters are the prey of many animals. The minute larvæ, as they swim about, are probably swallowed by everything which has a mouth large enough to admit them; and, as soon as the young oysters have become sedentary, they are eaten by everything which has jaws strong enough to crush them. Ground fishes, such as rays and fish of the cod tribe, easily break them up when they have grown much larger; while starfishes swallow them whole. Even the half-grown oyster, with a shell strong enough to resist most teeth, and too big for the maw of an ordinary starfish, is not safe from the depredations of the dogwhelk (*Purpura lapillus*) and the whelk tingle (*Murex erinaceus*), which effect a burglarious entrance, by means of the centre-bit with which nature has provided their mouths. It is very curious to watch a dogwhelk perched upon an oyster shell and patiently working, hour after hour, until the little and apparently insignificant tunnel, by which the insidious enemy will get access to the fat prey within, is completed. If you pull him off, he puts on as soft a look as the most innocent snail could do, as who should say, "Why prevent me from establishing closer intercourse with the dear neighbour at the other end of my tunnel?" The guardians of the oyster, however, who have not much of the "friend of humanity" about them, ruthlessly arrest the operations of the tunnellers by sudden squash with boot or hammer. And well they may, for they have few more dangerous adversaries. In the Bay of Arcachon, 14,000 whelk tingles were picked off 100 acres of oyster ground in the course of a month.

Other animals injure the oyster indirectly by mining in the shell.

The boring sponge, *Cliona*, does this ; and a very curious instance of mischief done in this way by a burrowing annelid (*Leucodore*) was recently brought to my notice by Sir Henry Thompson. The *Leucodore* drives burrows into the shell and lives in them without any evil intent towards the oyster. But the burrows fill with fine mud, and this, spreading into the vacuities of the shell, give rises to inky patches which look unpleasant when the oyster is opened and damage its commercial value, though, as I can testify, the flavour of the oyster is nowise impaired.

The larval oysters are extremely sensitive to cold, and any sudden fall in the temperature of the air during the swarming time is fatal to them. Even the adult oyster is readily killed by sudden frosts, if the water is sufficiently shallow to allow the change of temperature to penetrate. Great heat is equally pernicious. At Arcachon, immense numbers of oysters were killed by the hot summer of 1870.

To this long list of influences against which every oyster has to struggle successfully, if it is to attain maturity, larger knowledge will doubtless add many others. But these are enough to enable us to understand why it is that the increase of a given stock of oysters may be, and usually is, very slight, notwithstanding the prodigious fertility of the individual oyster. A very large proportion of the oysters in a bed, under ordinary circumstances, breed during the season ; and, as each adult female oyster, on an average, gives rise to a million eggs, one would expect a prodigious increase, even if nine-tenths of the young were destroyed. But from the small proportion of half-grown to full-grown oysters (40–50 per cent.) it is clear that the real addition to the oyster population, in most years, is very small. It is probable, in fact, that unless the conditions are unusually favourable, not more than two or three out of every million of the fry of the oyster ever teach maturity.

It is obvious that the conditions of existence of the oyster are of an extremely complicated character, and that the population of an oyster bed, under natural conditions, must be subject to great fluctuations. A few good spatting years, accompanied by a falling off in the number of starfishes and dogwhelks, may increase it marvellously, while the contrary conditions may as strikingly reduce it.

Man interferes with this state of things in two ways. On the one hand he is one of the most efficient of destroyers, and on the other, he is the only conservator of the mollusks, albeit his conservation is with a view to ultimate destruction. Let us consider him first under

the aspect of destroyer. In some places, oysters are taken at low tide by the hand; but usually they are captured by means of the dredge, which is essentially a bag, the sides of the mouth of which are fashioned into scrapers. The dredge is drawn slowly over the oyster bed for a certain time, and the oysters, with multitudes of other animals, stones, and the like, are scraped into the bag. This is then hauled up, and the contents emptied on to the deck; the oysters are picked out and the refuse is returned to the sea.

There can be no doubt that the great mass of oysters in an oyster bed may be removed by systematic and continuous dredging. But those who are best acquainted practically with the nature of that operation will be least inclined to believe that all the oysters on a bed could be cleared off in this way, even if the attempt were made; and, as it must cease to be profitable to dredge long before the point of entire clearance is reached, it is plain that, in practice, the attempt will not be made. It may be doubted if ordinary dredging ever fails to leave some thousands of oysters, great and small, on a bed of any extent.

Thus, if we admit, for the sake of argument, that an oyster bed may be exhausted by ordinary dredging, the reason why the oysters vanish is not obvious. For, supposing only a thousand oysters left, they ought to suffice to restore the bed by degrees. I am aware that it is said that, in the meanwhile, the enemies and competitors of the oyster have got the upper hand, that the ground has been spoiled by accumulation of mud and so on. But this reasoning leaves out of sight the fact that the oysters have not been there from all eternity. There was a time when there were no oysters on the ground, and when the oyster larvæ immigrated, fixed themselves there, increased and multiplied, in spite of all obstacles. Why should they not do so again?

The question is further complicated by the consideration that it is by no means certain whether the population of a given oyster bed is kept up by the progeny of its own oysters or by immigrants. As I have pointed out, it is ascertained that the larvæ, even under very unfavourable circumstances, may swim about for a week; and it has been estimated that they are ordinarily locomotive for two or three times that period. Even if we suppose the average period of freedom to be not more than three days, the chance that an oyster larvæ will eventually settle within a mile of the spot at which it was hatched in any estuary or in the open sea, must be very small. For, in an estuary, and almost always in the sea, one of the two alternating currents of water is dominant, and a floating body will drift, on the whole, in that direction, often many miles in the course of a day.

The opportunity of observing the natural formation of a new oyster bed is rare, but the details of the process have been carefully watched in at least one case. Up to the year 1825, the Limfjord in Northern Jutland consisted of a series of brackish water lakes communicating with one another, and opening on the east into the Kattegat. In the last century, unsuccessful attempts were made to plant them with oysters. But, on the 3rd of February, 1825, a great storm broke through the dam which separated the western part of the Limfjord from the North Sea; in consequence of this, the water of the fjord became gradually salter, the brackish water plants and animals disappeared and North Sea animals took their places. Among these, in 1851, oysters were observed, and, year by year, they extended over a larger area. In 1860, only 150,000 were taken; at present, there are ninety-eight beds, and, in 1871–1872, 7,000,000 of full-grown oysters were exported. There could have been very few oysters before 1851, when the first were noticed. But supposing the first entered as early as 1840, then, in thirty years, they spread themselves over an area of about sixty-four English miles, so that every year, on the average, they advanced more than two miles. The oyster beds are, at present, three-fifths of a mile to five miles apart, so that the larvæ must have been able to wander for at least five miles.[1]

During this slow process of immigration, it is obvious that the enemies and the competitors of the oysters had just as good a chance as the oysters themselves; and yet the latter have established themselves with great success. Why should they be unable to do the like elsewhere?

I must confess myself unable to arrive at a conclusion on the question whether what is called "overdredging"—that is, dredging to the extreme limit at which it is commercially profitable to dredge—is alone competent permanently to destroy an oyster bed or not. That oyster beds have disappeared after they have been much dredged, I do not doubt. But the commonest of all fallacies is the confusion of *post hoc* with *propter hoc*; and I have yet to meet with a case in which it is proved by satisfactory evidence, that an oyster bed has been permanently annihilated by dredging, when the spatting seasons have been good, and when there has been no reason to suspect an inroad of destructive mollusks or starfishes.

Man intervenes in favour of the oyster by the process which is known as "oyster-culture." This consists in collecting the spat as soon as it has attached itself, and removing it to conveniently-

[1] Mobius. *Die Auster und die Austern-wirthschaft*, p. 52.

situated natural and artificial shallows, known as "oyster-parks," where it can be protected from its enemies, and at the same time nourished.

Practised at Whitstable and elsewhere from time immemorial, this process has more recently been developed by laying down fascines of twigs, or tiles, in the way of the oyster larvæ during the spatting season. In good spatting years, the quantity of young oysters obtained in this way is prodigious. In 1865, Mr. Nichols, the foreman of the Whitstable Company, told the Sea Fisheries' Commissioners, that, in the year 1858, the spat was very abundant, and that the brood gathered in that and the three following years formed the stock from which the market had ever since been supplied. But he added, that they did not expect a good spatting season more than once in every six years; and that within his recollection, there had been no spat upon the flats, where it is usually collected, for a period of thirteen consecutive years.

It will be observed that oyster culture is not oyster breeding, but simply a means of profiting by the abundant produce of those years in which the young successfully reach their fixed stage. The supply is therefore very precarious. Moreover it is by no means easy to find localities suited for oyster-parks, which must be protected from storms, and yet have free access to the sea; shallow, and yet not liable to become too hot in summer or too cold in winter; open to currents which bring nutriment, and yet not liable to be silted up by mud. Even when all these conditions are fulfilled, much labour and watchfulness are needed to keep the beds clean and free from the incursions of enemies. And, when all that skill and industry can do is done, ostreiculture is attended with no less risk and uncertainty than agriculture in a variable climate. Favoured by one or two fortunate spatting years, M. Coste made ostreiculture the fashion a quarter of a century ago. A large capital was embarked, in France and in this country, in establishing oyster-parks, but it may be questioned whether more than a small fraction of the investment has ever found its way back into the pockets of the investors; and, in many cases, the results have been disastrous.

The increasing scarcity and dearness of oysters were subjects of complaint twenty years ago, and the outcry has become louder of late years. Three causes, and only three, so far as I know, have been assigned for this unsatisfactory state of things: first, the increase in the demand for oysters, owing in large measure to modern facilities of transport, consequent upon the vast development of the means of

locomotion; second, an unusual succession of bad spatting years; third, over-dredging, that is to say, the removal of so many oysters from the oyster beds that the number left is insufficient to keep up the stock.

That the first and the second of these causes have had a great deal to do with the matter is beyond doubt; but, whether any harm has resulted from simple over-dredging is a question respecting which very different opinions are entertained, and I have already stated my reasons for reserving my opinion on the subject. But I shall suppose, for argument's sake, that all three influences are in operation, and proceed to ask what can be done by legislation to mitigate their evil effects.

A sumptuary law restricting the consumption of oysters, per head, is not practicable in these days; and therefore the first cause of dearness, great demand, must be left to cure itself by the increase of price to which it gives rise.

Nor is the second cause of scarcity within reach of legislation. The seasons cannot be rendered favourable to oyster spatting by Act of Parliament.

But it is very generally believed that the enforcement of what is called a "close time" is an effectual remedy for over-dredging. Oyster "close time" means that oysters shall not be taken during the months of May, June, July, and August, which are supposed, not quite accurately, to cover the breeding season of the shell-fish.

But, surely, nothing is more obvious than this, that the prohibition of taking the oysters from an oyster bed during four months of the year is not the slightest security against its being stripped clean (if such a thing be possible) during the other eight months. Suppose, that in a country infested by wolves, you have a flock of sheep, keeping the wolves off during the lambing season will not afford much protection if you withdraw shepherd and dogs during the rest of the year.

These considerations are so obvious, that I cannot but think that the cry for close time for oysters must be based on a confused notion that, as close time is good for salmon, so it must be good for oysters. But there is really no analogy between the two things which here pass under the name of "close time." Close time for oysters is merely protection of oysters during the breeding season, close time for salmon is not merely protection of salmon during the breeding season, it means a practical limitation of the capture of salmon all the year round by the weekly close time, supplemented by the license duties on rods and nets. You might protect the breeding grounds of salmon

as strictly as you pleased and as long as you pleased ; but, if too many of the ascending fish were captured, the stock would fall off, and if all were captured, it would come to an end.

If the protection afforded to an oyster bed is to be made equivalent to that given to a salmon river, measures must be taken by which the undue diminution of the stock of oysters, at any time, may be prevented. The most effectual way of doing this is to form an estimate of the number of oysters on a bed before the commencement of the open season ; and to permit the removal of only such a percentage as will leave a sufficient stock. And regulations of this nature have long been carried out in the Schleswig oyster fisheries and in those of France. A subsidiary regulation, tending towards the same end, is that which enforces the throwing back into the sea of all half-grown oysters. As oysters produce young before they are half-grown, this procedure must contribute to the breeding stock.

When, nearly twenty years ago, my colleagues, Sir James Caird, Mr. Shaw-Lefevre, and I, had to deal with the oyster question, I am not aware that any of us doubted the value of protection of public oyster beds in the open sea, if it could only be made efficient.

What we were quite clear about, however, was :—

(1) That the close time regulation which then existed was always useless, and sometimes mischievous.

(2) That the regulation prohibiting the taking of half-grown oysters interfered with the transfer of oysters from the public beds, where they were exposed to all sorts of dangers, to the private grounds where they were protected.

(3) That it was practically impossible to establish an efficient system of protection on our public oyster beds.

And therefore we came to the conclusion that the best course that could be adopted was to abolish all the delusive and vexatious regulations which were in force ; and to see what could be done by giving such rights of property in parts of our shores favourable to oyster culture, as would encourage competent persons to invest their money in that undertaking.[1]

[1] "10. We have made diligent inquiry into the condition of the oyster fisheries, and have devoted a large section of our report to the discussion of the evidence which we have obtained. We find :

"That the supply of oysters has very greatly fallen off during the last three or four years.

"That this decrease has not arisen from over-fishing, nor from any causes over which man has direct control, but from the very general failure of the spat or young of the oyster, which appears, during the years in question, to have been destroyed soon after it was

Our recommendations were carried out. But as the complaints about the scarcity of oysters went on increasing, the matter was re-investigated by a Committee of the House of Commons in 1876. This Committee published two reports, a valuable minority report by Mr. Shaw-Lefevre, and a singular majority report drawn up by the chairman.

The latter states that the Committee " have come to the conclusion that the supply of oysters round the British coasts has for some years steadily decreased; and that, though, to some extent, cold seasons have contributed to cause this diminution, the principal cause is to be found in the continual and constantly increasing practice of over-dredging for them in open waters, without allowing sufficient close time. Your Committee have also obtained evidence from France, in which country regulations for close seasons, for some years, have been more or less rigidly insisted on: and it appears to them that, in proportion to the stringency with which these regulations have been enforced, the supply of oysters has increased.

"Your Committee have therefore come to the conclusion that it is desirable to make provision for a general close time for oyster fisheries, and that it should extend from the 1st of May to the 1st of September in each year."

In consequence of this recommendation we have got back the old close time; which, as I hope I have already sufficiently proved, is of not the slightest value for the purpose which the Committee intend it to serve.

It will be observed that the Committee attach much weight to the evidence received from France. It is undoubtedly very weighty; but I think that if the Committee had given it the attention which it deserves, they would have seen that it tells dead against their recommendation.

produced. A similar failure of spat has frequently happened before, and probably will often happen again.

"That the best mode of providing against these periodical failures of the spat is to facilitate the proceedings of those individuals or companies, who may desire to acquire so much property in favourably situated portions of the sea bottom, as may suffice to enable them safely to invest capital in preparing and preserving these portions of the sea-bottom for oyster culture. By which term 'oyster culture' is implied, not the artificial breeding of oysters in the manner in which salmon are bred artificially, but the collection of the brood in years when that brood is plentiful and its preservation by the application of due skill and care, as a source of supply during the years when the spat fails—a process in vogue among British fishermen from time immemorial.

"That no regulations or restrictions upon oyster fishing, beyond such as may be needed for the object just defined, have had or are likely to have any beneficial effect upon the supply of the oysters."—*Report of the Commissioners appointed to inquire into the Sea Fisheries of the United Kingdom*, 1866.

In the first place, the Committee do not seem to have noticed that the French regulations involve, not merely a breeding season close time, such as they recommend, but that they restrict the fishing during the open season to a few days, or stop it altogether, at the discretion of the administration. The difference of the two systems is that the French regulations are adequate for the purpose of preventing over-dredging, while the English regulations are not; and that is a somewhat essential difference.

But there is another point of still greater importance, which is, that a careful study of the French statistics, and of the very excellent reports on the various French oyster fisheries made to the Committee by Mr. Hall, leaves it very doubtful whether the French system of protection, stringent as it is, has had any appreciable effect on the fisheries.

Let us take the case of the famous oyster fishery of Cancale. Mr. Hall says in a noteworthy passage of his Report, which, one would think, the majority of the Committee can hardly have considered with due care :—

"The oyster beds of Cancale and Granville extend over that part of the bay of Mont St. Michel which lies beyond extreme low-water mark, and as far out as the Iles Chaussey; they also stretch for six or eight miles along the coast north of Granville. They are remarkable as presenting instances of beds existing under identical natural conditions, subjected to identical regulations, and offering results of a very varied kind. *They are also interesting as being beds which, notwithstanding the enforcement of preservative regulations for a considerable number of years, have become, on the whole, unproductive.*

"There appears to have been no time since 1853, when the observance of the close season, a limitation of the fishing during the other months in greater or less degree, and the prohibition of the removal of undersized oysters, except to the *étalages*, or storing beds of the neighbourhood, have not been enforced at Cancale." [1]

The bay is marked out into a series of beds, named from west to east, Bas de l'Eau, Corbières, Vivier-ô-le Mont, La Raie, St. George, Beauvais-ô-le Mont; while, beyond the last, is a large area left as a reserve and not allowed to be fished.

From 1862 to 1866, inclusively, hardly any spat was observed in the bay. In 1866, the northern part of the Raie bank, which had already shown some signs of increase in 1865, produced a considerable spat. In 1867, it was fished and yielded 1,007,000 oysters. But, in

[1] *Report of the Select Committee on Oyster Fisheries, 7th July,* 1876, Appendix, pp. 260 and 261.

the following years, so large a number of dogwhelks showed themselves upon it, that it was thought better to fish the bed than to let the oysters be fruitlessly destroyed. The dogwhelks were cleared away and the bank, which, though much thinned, still held oysters, was left to rest in 1870. In 1871, however, all the oysters had disappeared, while cockles had taken their place, and remained up to the time of the report.

In 1871, the southern half of the Raie bank, which had produced no oysters since 1862, showed so many, that in 1871–72 it yielded a crop of 2,070,000; and from that time, though fished in alternate years, it became the richest bed in the bay, and, in 1876, showed a large quantity of brood over its whole extent. While the southern half of La Raie thus became productive, St. George, which adjoins it and from which it probably derived the colony which peopled it in 1869, became sterile, without any apparent cause. That it had not been over-fished was evident from the fact that a large number of oysters still existed upon it. No spat, however, had been seen on St. George since 1874.

On the other side of La Raie, the southern half of Vivier-ô-le Mont, which touches the southern part of the former, and on which no fall of spat had taken place since 1862, showed a fair quantity in 1872, before the newly imported oysters in La Raie had had time to spread themselves over it, and, up to 1876, it was fairly productive. On that part of Beauvais-ô-le Mont which was productive in 1876, more or less production has always taken place.

No spat has ever been observed on the reserve ground, and in 1876 it was tenanted by only a few old oysters. Cultch has always been abundant, and cleaning by trawling has been permitted since 1867.

It will be observed that under the same conditions, and subject to restrictions of a stringency which no one has dreamed of in the public oyster beds of this country—a fertile area (La Raie, N.) has become barren, and a barren area (La Raie, S.) has become fertile; while the others (Viviers and Beauvais), after undergoing great impoverishment are rather more productive at the end, than at the commencement of the period of fifteen years. And all this time, the oysters have perversely refused to settle upon the ground kindly reserved for their reception by the administration.

The history of the oyster fisheries of Arcachon is not less instructive.

The Bay of Arcachon may be almost said to be made for oysters. It has the shape of an equilateral triangle nine or ten miles on the

TABULAR VIEW OF THE OYSTER FISHERY IN THE BAY OF CANCALE,

BETWEEN 1860 AND 1875.

The numbers in brackets represent the number of tides during which fishing was permitted. In 1873-4 *the fishings of Corbières, Viviers, and La Raie* (*s*), *and in* 1874-5 *those of Bas de l'Eau, Corbières, and Viviers, and those of St. George and Beauvais are not given separately.*

	BAS DE L'EAU. (S.W.)	CORBIÈRES.	VIVIERS.	LA RAIE. (S.)	LA RAIE. (N.)	ST. GEORGE.	BEAUVAIS. (N.E.)
1860-61	......	1,945,260 (6)	......	......	......	......	......
Hardly any Spat. 1861-62	6,200,600 (3)	2,800,400 (2)	No Spat. 3,460,600 (3)	......	......	......	1,220,000 (4)
1862-63	1,020,000 (3)	......	109,300 (1)	......	539,150 (2)	643,300 (2)	111,500 (3)
1863-64	......	840,000 (3)	1,504,000 (4)	O	......	......	390,000 (3)
1864-65	......	......	......	O	108,000 (1)	109,000 (2)	658,000 (3)
1865-66	200,000 (2)	155,000 (1)	176,000 (2)	O	Spat.	......	......
1866-67	......	......	667,000 (2)	O	Dogwhelks. 1,007,000 (2)	......	......
1867-68	......	......	......	O	860,000 (3)	411,000 (2)	......
1868-69	......	188,000 (1)	215,000 (2)	O	370,000 (1)	220,000 (1)	340,000 (2)
1869-70	......	......	......	Spat.	O	......	1,642,000 (2)
1870-71	......	......	......	......	Cockles.	1,650,000 (4)	......
1871-72	......	......	Spat.	2,070,000 (2)	"	780,000 (1)	1,038,000 (2)
1872-73	......	......	3,560,000 (3)	......	"	No Spat. 2,140,000 (2)	1,600,000 (4)
1873-74	......		7,350,000 (5)		"	......	1,766,000 (4)
1874-75		5,070,000 (3)			"	4,272,000 (4)	

side; and it debouches by a channel, thirty fathoms deep at the mouth, situated at its northernmost angle, into the Bay of Biscay. The winds and waves of this stormy region have thrown up a range of high sand dunes along the western boundary, and these dunes, covered with pines, shelter the bay from the violence of the westerly gales. The difference of height between high and low water (ordinary tides) is fifteen to sixteen feet. At flood tide, the whole surface of the bay, except an island in the middle (Ile des Oiseaux) is covered, but, at ebb tide, the greater part is dry, except in so far as it is traversed by narrow channels, varying from forty to ten feet in depth, formed by the water as it retires into the deep outer passage at the ebb, and returns at the flood.

The interspaces between the channels thus laid bare at each ebb are called "cressats." The bottom is composed of sand and shells with more or less mud. The quantity of the latter constituent is said to be gradually increasing; and, in many parts, old oyster beds are silted up and covered with mud. The salinity varies, being least in the northern angle, where much fresh water flows in. Elsewhere the saline constituents amount to 3 per cent or more, and in hot and dry seasons they may exceed those of the Atlantic water outside.

M. Tolle says, in his report to the German Government on the oyster fisheries of France—

"The cressats are the old oyster beds of Arcachon, once thought to be inexhaustible, which yearly yielded seventy to seventy-five million oysters of different kinds and sizes, of the value of 225,000 francs. But in course of time, especially between 1830 and 1840, the demand becoming greater and oysters scarce, they were so exhaustively fished, that in the year 1840 the produce was only 1,000 francs" (*Bericht*, p. 9).

According to this, the produce of the beds before 1830 was 75,000,000 yearly, while in 1840 it had sunk to 330,000, or thereabouts, that is less than $\frac{1}{200}$th of the previous yield.

"It was only after this almost complete exhaustion of the beds that the Government took means to prevent their furthur destruction. The Prefect of the Arrondissement sent a vessel to watch the beds, and enforce the strict observance of the law. But too late. The attempts of private persons to repopulate the beds also failed. This condition lasted till 1859."

In 1860, however, at M. Coste's suggestion, two parks, on the *Crastorbe* and *Grand Cès* cressats (north of the Ile des Oiseaux) were established by the Government; and, in the following year, numerous

concessions were made to private individuals. These were stocked with oysters, so that, between 1859 and 1861, 15,000,000 of oysters were laid down in the parks.

Such is the account given by Tolle and Möbius. But I am wholly unable to reconcile the assertion that the natural beds had failed before 1860, with the statistics given by Mr. Hall in his already cited report. Mr. Hall states that, in the year 1860–61, no fewer than 19,900,000 oysters were fished on the natural bed. Hence it follows that in 1859–60 there must have been at least 19,900,000 half-grown oysters, and in 1858–59 at least the same number of one-year oysters, and, therefore, that there must have been a fall of spat sufficient to produce these in the preceding season. And, in fact, Mr. Hall states that, in 1857–8, there was an "abundant" spat, and that the weather during the spatting months was "fine." Mr. Hall further observes that, until 1860–61, "no register was kept of the produce of the natural banks," so that nothing is accurately known of the yield of the beds in 1857–58, or the subsequent years up to 1860–61.

Now it is to be observed that, in these years, as in those which preceded them, fishing was "permitted without restriction from the first of November to the first of April," the only condition being that oysters less than five centimetres (about two inches) across must not be taken; and it was only in 1860–61 that the new restrictive regulations came into force, the fishing being limited to not more than fourteen days in the whole season, and less than three hours in each day, on the average.

And what followed upon the adoption of these severe regulations? Simply that for five years the oysters on the natural beds steadily and rapidly diminished.

In 1861–2	19,000,000	were taken.
1862–3	15,097,320	"
1863–4	5,154,170	"
1864–5	2,697,460	"
1865–6	2,012,940	"

Then comes a very slight improvement—

1866–7	3,266,730	"
1867–8	3,711,730	"
1868–9	3,648,230	"

In 1870, a large number of oysters were killed on the beds by the great heat of the summer, and no fishing was permitted.

But instead of any falling off, the next year shows a manifest increase—

1870–1 4,997,540

After this the beds were fished only in alternate years and yielded

1872–3 7,441,720
1874–5 40,360,000

The outcome of all this is that, under one continuous system of extreme restrictive regulation, the returns show:—

1st. For five years (1861–66) a rapid decrease, down to a ninth of the produce of 1860–61, which was the end of a long period of slight regulation.

2nd. For five years (1867–71) a slight and slow increase up to about one-fourth of the produce of 1860–61.

3rd. For five years (1870–75) an increase rising in the last year, 1875, to 40,360,000 (that is to say, seeing that 1874 crop was not fished, 20,000,000); or, practically, the same yield as that with which the fifteen-year period started.

It is certainly astonishing to have this case held up as an example of the efficiency of regulations and especially of the enforcement of close time.

Thus, even if the open sea oyster beds could be watched and protected as efficiently as those of the bays of Cancale and Arcachon, such protection is no guarantee against the greatest fluctuation in the produce of the beds, and the disappearance of the oysters from some of them. But who that knows anything practically of the manner in which the open sea oysters leads are fished, can imagine that any such protection is practicable? Is the Government to survey the oyster beds every summer and then send a gunboat to watch every oyster bed, and limit the quantity of oysters taken? And if it does not do so, what is to prevent the clearing of every open sea bed (so far as it can be cleared) during the open season? Or, suppose a law to be passed prohibiting the capture of undersized oysters, is it better to leave these oysters to take their chance of becoming the prey of dogwhelks and starfish; or to remove them to safe and sheltered parks?

I have not yet been able to obtain answers to these questions in a sense favourable to protective legislation, from any one practically conversant with the facts of the case. People rave about protection

and when you ask them how they propose to give any real protection to open sea beds they cannot tell you.

I for my part believe that the only hope for the oyster consumer lies first in oyster culture, and secondly, in discovering a means of breeding oysters under such conditions that the spat shall be safely deposited. And I have no doubt that when those who undertake the business are provided with a proper knowledge of the conditions under which they have to work both these objects will be attained.

XXXV

PRELIMINARY NOTE ON THE FOSSIL REMAINS OF A CHELONIAN REPTILE, *CERATOCHELYS STHENURUS*, FROM LORD HOWE'S ISLAND, AUSTRALIA.

Proceedings of the Royal Society of London, vol. xlii., 1887, *pp.* 232–238.
(*Read March* 31*st*, 1887.)

THE interesting remains of which I propose to give a brief notice in the present communication, are contained in a friable sandstone (apparently formed of concreted blown sand), and they have a very recent appearance. The age of the deposit in which they are found is unknown, but it is probably quaternary. The specimens have been for some years in the palæontological collection of the British Museum; and, for the most part, they have not yet been submitted to careful examination. But I learn that the greater number of them were long since rightly determined to be Chelonian by Mr. Davis, and set aside as such.

Several of the most important of these numerous and, in general, very fragmentary bones were originally found imbedded close together in the same block of sandstone. They consist of a great part of a pelvis, a caudal vertebra, and an imperfect skull. Of the pelvis, a right ischium and a pubis are imbedded in the rock, while an imperfect right ilium, which fits well on to the ischium, is separate; all these bones are unmistakably Chelonian. The caudal vertebra has remarkable peculiarities. It resembles an ordinary Chelonian caudal vertebra from the anterior half of the tail, in its general characters; but it is strongly opisthocœlous, the centrum having a deep cup behind and a correspondingly curved articular head in front. From the posterior part of the ventral face, two stout processes diverge, and present terminal rounded facets for the rami of the large chevron bone which must have articulated with them. As a general rule,

the caudal vertebræ of Chelonia are procœlous—but *Chelydra* and *Gypochelys* (perhaps also *Staurotypus* and *Platysternum*) form well known exceptions,[1] in so far as the vertebræ behind the 3rd or 4th are strongly opisthocœlous. In fact, the vertebra in question closely resembles the 6th or 7th of *Chelydra* or of *Gypochelys* (see figs. 1 and 2). In the first, however, the transverse processes are very much stronger and the pentagonal platform into which the upper surface of the neural arch expands, in place of a neural spine, is as long as the

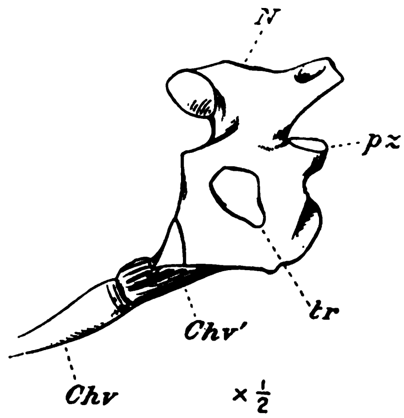


FIG. 1.—Caudal vertebra of *Ceratochelys*. *N*, platform on the neural arch; *pz*, prezygapophysis mutilated; *tr*, broken transverse process; *Chv'*, processes for the chevron bone; *Chv*, chevron bone.

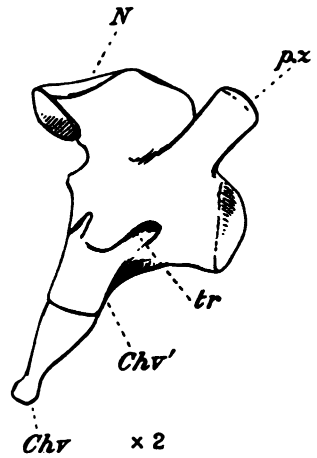


FIG. 2.—Caudal vertebra of *Chelydra*. Letters as in Fig. 1.

vertebra, instead of being only about half as long. The stout prezygapophysis of the right side is broken off, leaving only the base visible in the fossil.

[1] The opisthocœlous character of most of the caudal vertebræ of *Chelydra* was first pointed out by Von Meyer in his description of the Œningen *Chelydræ*. Baur ("Osteologische Notizen," 'Zool. Anzeiger,' No. 238, 1886) has gone fully into the question, and has pointed out the exceptional nature of their structure among the Chelonia. Since the above paragraph was written, Dr. Gunther has kindly enabled me to examine a spirit specimen and a skeleton of *Platysternum*. The caudal vertebræ resemble those of *Chelydra*, except that the last nine are procœlous, while that between these and the more anterior opisthocœlous vertebræ is nearly flat at the ends. In this, as in other respects, *Platysternum* presents characters intermediate between *Chelydra* and the ordinary *Emydæ*. Professor Cope ('Vertebrata of the Tertiary Formations of the West,' 1883, p. 111) ascribes opisthocœlous caudal vertebræ to the *Baenidæ*, but no figures or descriptions of such vertebræ are given. Of the opisthocœlous Chelonian vertebræ figured in Plate XXIV of the 'Report of Extinct Vertebrata obtained in New Mexico' (1877) it is expressly stated that their "correct reference cannot now be made" (p. 43).

Two other caudal vertebræ, having the same structural features, occur among the detached remains; and belong, like the first, to the second fourth of the tail. Another tolerably complete vertebra, with a considerably longer centrum, corresponds very closely with a caudal vertebra of *Gypochelys* from the third fourth of the tail. In this, as in one of the foregoing vertebræ, the chevron bones are ankylosed with the centrum. I conceive, then, that there can be no doubt that the pelvic bones and these caudal vertebræ belonged to a Chelydroid Chelonian, of about the size of the largest "Snapping turtles" which are met with in North America at the present day.

Prima facie, the skull found in the same block might also be expected to be that of a Chelydroid; and, in fact, it is so. I do not base this interpretation on the Chelonian character of the upper jaw, as there are various extinct Saurian reptiles which closely approximate Chelonia in this part of their structure. The diagnostic characters lie in the back part of the skull; and especially in the auditory region, which is altogether Chelonian. Not only so, but when this fragmentary skull is compared with that of *Chelydra*, the correspondence between the two is singularly exact (figs. 3 and 4). In two respects, however, the fossil differs from *Chelydra* and *Gypochelys*.

1. The roof over the temporal fossa formed by the parietal, post-frontal, and other bones, which leaves the auditory region uncovered in the recent genera,[1] extends back, beyond the occiput, in the fossil, and sends down a broad vertical rim from its margin.

2. The upper surface of the cranial shield is, at most, rugose in the recent *Chelydridæ*; in the fossil, three strong conical processes, like horn-cores, of which the middle is the longest, are developed from its posterior and lateral region.[2]

This skull is described and figured in the 'Philosophical Transactions' for 1886 (Plate 30, fig. 1) by Sir R. Owen, under the generic or subgeneric name of *Meiolania*, and is said to belong to a Saurian reptile closely allied to the "*Megalania prisca*" described in earlier communications. But the skull is assuredly that of the Chelydroid Chelonian to which the pelvis and caudal vertebra belong. What *Megalania prisca* may be I do not pretend to say; but the remains which I have described can have nothing to do with any Saurian reptiles; and I propose to confer on the genus of Chelonia to which they belong the name of *Ceratochelys*.

The singular osseous caudal sheaths described by Sir R. Owen, in

[1] The 'roof' extends much further back in *Platysternum*.

[2] It is possible that these may be dermal bones coherent with the proper cranial shield.

the same memoir, also appertain to *Ceratochelys*. They formed part of the series of remains sent to the British Museum along with the foregoing, in which none but Chelonian bones have yet been discovered; and the remains of vertebræ left in these sheaths are similar to the caudal vertebræ of the terminal fourth of the tail in the *Chelydridæ*. The Snapping turtles are noted for the length and strength of the tail and for the strong, laterally compressed,

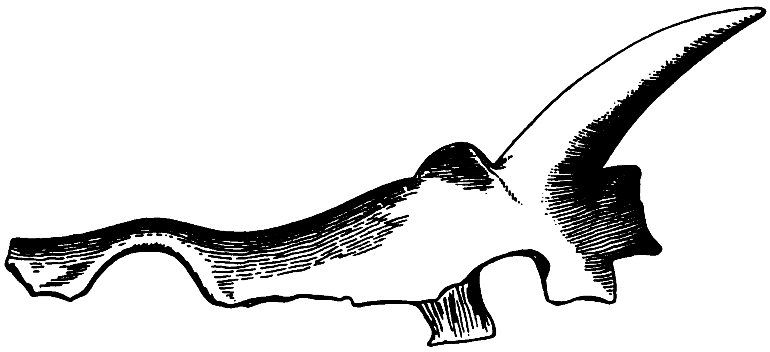


FIG. 3.

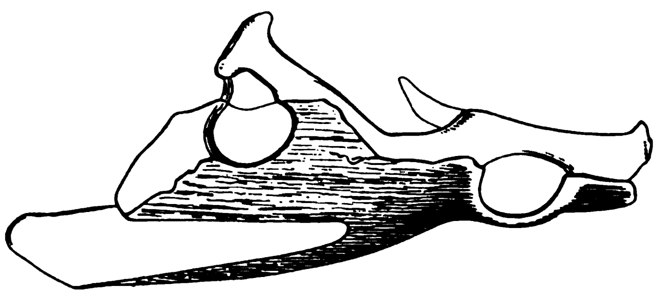


FIG. 4.

Skulls of *Ceratochelys* (fig. 3) and *Chelydra* (fig. 4); the latter of the natural size, the former much reduced. The portion of the skull of *Chelydra* which corresponds with the fossil is shaded.

acuminated "scales" which form a crest along the median dorsal line, while others, less strongly keeled, lie at the sides of the tail. In many Chelonia, the extremity of the tail is enveloped in a continuous sheath. These and other scale-like structures in the Chelonia are usually spoken of as if they were entirely epidermal. But, a day or two ago, Dr. Günther informed me that in the Australian Tortoise *Manouria*, the great imbricated scales of the limbs contain bony scutes; and that similar scutes are to be found in *Testudo græca*

This of course, suggested the examination of the caudal scales of *Chelydra* and *Gypochelys*; and, having been enabled by Dr. Günther's kindness to examine the caudal scales of a good sized specimen of the latter, I have found that those of the crest contain bony scutes.[1] The bony scute corresponds very closely in form with the whole "scale," but the recurved apex of the latter is formed only by epidermal substance (figs. 5 and 6).

The living *Chelydra*, therefore, has a caudal armature which, in principle, is similar to that of *Ceratochelys*, but the osseous elements are relatively atrophied. There is exactly the same relation between the armour of species of living *Crocodiles* and *Alligators*, on the one hand, and those of *Jacare* and *Caiman* and the extinct *Teleosauria*, on the other. In the former, the epidermal scales remain well developed on the ventral side of the body, while the corresponding osseous scutes, fully developed in *Jacare*, *Caiman*, and *Teleosauria*, have vanished.

Among the detached fragments to which I have referred, there are remains of ribs, with their costal plates; marginal and other plates of the carapace; parts of the plastron; part of a scapula; sundry limb bones; and several of the cranial processes called "horn-cores." They all agree, so far as they can be compared, with the determination already arrived at; which, to sum it up in a few words, is that the remains of crania and caudal sheaths from Australia, hitherto referred to Saurian reptiles, under the names of *Megalania* and *Meiolania*, appertain to a hitherto unknown species of Chelonian, *Ceratochelys sthenurus*, closely allied to the living *Chelydra*, *Gypochelys*, and *Platysternum*.

The evidence of this fact offered in the present note appears to me to be conclusive, but it may be desirable hereafter to figure the parts mentioned and to describe them at length.

The interest which attaches to the discovery of this singular Chelonian arises partly from the fact, that the group of Chelonia to which it belongs is wholly unrepresented in the fauna of Australia, as at present known. *Platysternum* is usually said to be found in China. Dr. Günther, however, informs me that Upper Burmah is its proper habitat; otherwise, North America, east of the Rocky Mountains is the nearest region in which the *Chelydridæ* are to be found. But *Chelydridæ*, and, indeed, species of the genus *Chelydra*, occur in

[1] The fact is noted by Rütimeyer (Lang and Rütimeyer, "Die Fossilen Schildkröten von Solothurn," 'Denkschriften der Allg. Schweiz. Gesellschaft,' vol. 22). The armature of the tail in *Platysternum* is for the most part arranged in zones, of four plates in each zone; but I have not yet been able to find any bone in them.

Upper Miocene (Œningen) and in Eocene formations in Europe. Moreover, *Platychelys*, of the Upper Jurassic series of Bavaria and Switzerland, is regarded by Rütimeyer as an early form of the group.

Lord Howe's Island is about 200 miles from the nearest Australian mainland, and something like 400 miles, as the crow flies, from the Darling Downs, in which the caudal armour, which has been ascribed to *Megalania*, was found. The discovery of *Ceratochelys*, therefore, has an interesting bearing on the question of the former extension of Australia to the eastward, on the one hand; and of the possible derivation of such forms as *Ceratochelys* from Asia, on the other hand

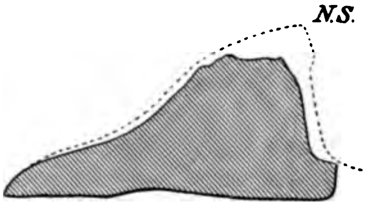


FIG. 5.

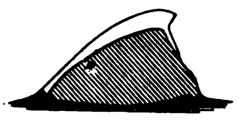


FIG. 6.

Sectional views of a scute of the tail-armour of *Ceratochelys* (fig. 5), and of one of the crest plates of *Gypochelys*, both of the natural size.

An elevation of the sea bottom of 6,000 feet would place Norfolk Island and Lord Howe's Island on a peninsula extending from the region of the present Barrier Reef to New Zealand; and the Floræ and Faunæ of those islands are known to have special affinities with those of New Zealand and none with those of Australia.

Speculations respecting the origin of the Chelonian carapace are suggested by the discovery of osseous scutes in the vertebral region of the tail, and their coalescence in *Ceratochelys* to form a sort of caudal carapace, ridged in a manner resembling that of *Chelydra* and *Platychelys*. But the consideration of these points would take me beyond the limits of the present note.

XXXVI

THE GENTIANS: NOTES AND QUERIES.

The Journal of the Linnean Society, vol. xxiv., 1888, *pp.* 101–124.
(*Read April 7th*, 1887.)

(PLATE II. [PLATE 26]).

I HAPPENED to spend some six weeks, from the end of July to the beginning of September 1886, at Arolla (a locality situated at the head of one of the southern offshoots of the valley of the Rhone near Sion), 6,400 feet above the level of the sea. During my wanderings about the woods and pastures which clothe the sides of the valley from this level to the snow-line, a couple of thousand feet higher, my attention was attracted by the characteristically alpine vegetation, and more especially by the Gentians, of which some species, such as *Gentiana purpurea* and *G. campestris*, were very abundant. *G. verna* and *G. acaulis* were also by no means uncommon; but the latter had almost ceased to flower.

It is well-nigh forty years since I occupied myself with systematic botany; and I had no works of reference at hand except Gremli's 'Flore analytique,' which I happened to have bought at Lausanne, and Rapin's 'Guide des Botanistes dans le Canton de Vaud,' which a fellow-traveller was kind enough to lend me. But the extraordinary amount of variation which presented itself when I compared considerable suites of specimens with the diagnoses and descriptions in these works struck me so much that, all "unanointed and unannealed" as I was in systematic work, I was tempted to see what I could make out of the facts for myself. In truth, the Gentians took hold of me rather than I of them; and I have been more or less their bondservant ever

since. Beginning with *Gentiana purpurea*, I found that I could not understand that form without knowing something about the rest of the species of *Gentiana*; and, by a parity of reasoning, a knowledge of *Gentiana* involved that of the other genera of the Gentianeæ. So that since my return to England, I have been led to make a rapid survey of the whole Order; and it is the broad results of that survey that I wish to lay before the Linnean Society.

I have to thank the Director of Kew Gardens for the free use of the splendid herbarium under his charge. It affords the means of carrying out the investigation I have attempted much more thoroughly; and I am well aware of the incompleteness of the observations I venture to offer. But, at present, it is needful for me to turn my attention to other things; and if I venture to bring forward so imperfect a piece of work, it is in the hope that it may be taken up and finished by more competent hands.

Every botanist is aware that the Gentianeæ constitute one of the most natural and well-defined of the Orders of plants. The type of structure which runs through the five or six hundred species included in the Order undergoes but few and, for the most part, inconsiderable modifications. There are no trees and but few shrubs among them; a few are climbers; and there are a few saprophytes. The opposition, entirety, and palmati-venation of the leaves have but few exceptions; and it is very rarely that the flower departs from typical regularity. The chief distinctive characters of the groups into which the Order is at present divided lie in the flower, and indeed in the corolla; since the form and proportion of the calyx, the occasional synanthery, and the greater or less intrusion of the placentæ are characters which vary greatly from genus to genus.

Under these circumstances, I have confined myself almost entirely to the study of the structure of the flower. I find that some seven or eight modifications of that structure are distinguishable; and that these again fall into two series, each of which is characterized by a peculiar disposition of the nectarial organs, and presents a gradation of forms of the corolla from the rotate, or rather stellate, condition through the campanulate to the extreme infundibulate character.

In one of these series the nectarial cells are situated on the inner surface of the cup, from the edge of which the lobes of the corolla proceed, and towards its basal end. They are aggregated in such a manner as to form either a single patch, bisected

by the vein which becomes the median vein of a corolla-lobe; or two patches, one on each side of that vein. I term the Gentianeæ of this series *Perimelitæ.*

In the other series there are no such patches of secreting-cells visible on the corolla; but in many members of the series there is a zone of such cells, which encircles the base of the ovary, and is therefore furnished by the outer faces of the carpellary phyllomes, which are often raised into tubercles. In others, I have not been able to make sure of the existence of nectarial cells, either on the surface of the ovary or on the stemono-carpellary internode, which forms the actual bottom of the flower-cup. But dried plants are very unfavourable subjects for the determination of points of this kind; and as many of these flowers, which have no apparent nectaries, are known to be visited by honey-sucking insects, I shall for the present assume that honey-secreting surfaces exist on the central parts of the flower. In contradistinction to the *Perimelitæ*, the Gentianeæ of this series may be termed *Mesomelitæ.*

In the series of the *Perimelitæ* four modifications of floral structure are discernible. To these I propose to give the names of *Actinanthe*, *Keratanthe*, *Lophanthe*, and *Stephananthe.*

I. *Actinanthe.*

The corolla is rotate,[1] or, if it is more or less campanulate, the sinuses which separate the lobes are very deep. The nectarial areæ are single or double, and often concave inwardly. There is no distinct gynophore; but the ovary is occasionally "stipitate"; that is to say, its basal moiety, which then contains no ovules and remains very narrow, constitutes an apparent stalk on which the dilated ovuligerous moiety is supported. The margins of the lobes of the corolla may be produced into longer or shorter denticulations or laciniæ; but there are no filamentous appendages developed on the inner face of the corolla. The stigmatic surfaces are oblong-ovate.

[1] This term appears to me to be often employed ambiguously. It is applied on the one hand, to corollæ in which the cup appears to be formed merely by the confluence or connation of the bases of the lobes, and is not in any way marked off from the latter; and, on the other hand, to corollæ in which the cup more or less closely embraces the ovary, and is even narrower at the summit than the middle. The physiological import of the two forms is very different; and, morphologically, the latter are really hypocrateriform corollæ with very long lobes. I use the term "rotate" in the first sense.

The species in which I have found this type of floral structure are:—

A.	B.	E.
Gentiana	Gentiana.	Gentiana.
aurea.	primulæfolia.	saxosa.
umbellata.	vaginalis.	cerina.
Moocroftiana.	nummularifolia.	
detonsa.	saxicola.	
	multicaulis.	
Jæschkea.	incurva.	
Pleurogyne.	Grisebachii.	
Exadenus.	gracilis.	
	monieroides.	
	ericoides.	
	magellanica.	
	patagonica.	

In *Exadenus* the nectarial surfaces are hemispherically depressed and bulge outwards, so that their positions are marked externally by convexities of the corolla. Dr. Grisebach ('Genera et Species Gentianearum,' p. 322) says of each "fovea glandulifera," that it is "extus tantum conspicua, intus per petali substantiam clausa;" but the real state of the case appears to me to be as I have stated it. *Exadenus*, in fact, represents the first stage of a transition from *Actinanthe* to the next type.

II. *Keratanthe.*

This differs from the preceding in no essential respect, except in the deepening of the nectarial concavities, in such a manner that their external walls project as long horns or spurs which are sometimes directed downwards and sometimes upwards. Moreover, the lobes are relatively shorter, and the corolla is more or less campanulate. It is very possible, and indeed probable, that further inquiry may bring to light forms constituting a complete transition between *Actinanthe* and *Keratanthe*.

The genus *Halenia* is the only representative of this type.

III. *Lophanthe.*

Here, again, the corolla has fundamentally the same characters as in *Actinanthe*; and the only essential difference lies in the development of filamentous appendages, or fimbriæ, from the inner surface of its cup. These fimbriæ occur in different positions: sometimes they are *parastemonal*; that is to say, they arise singly or in groups from a common base,

along, or close to, the line of symphysis of the filaments of the stamens with the cup of the corolla. In this case they are sometimes so minute as to be distinguishable only by the aid of the microscope; sometimes, on the other hand, they are so long as to extend across the interval between one series and another, and thus to form a more or less complete barrier across the interval between the ovary and the corolla. These fimbriæ have already been noticed in some of the species in which they occur; but they have been described as appendages of the filaments of the stamens. I have looked into this point with considerable care; and, in all cases, I find that the fimbriæ cohere with the corolla and not with the filaments, if sufficient care is taken in separating the two. If the filaments are roughly torn away, on the other hand, some of the fimbriæ may come with them, attached by flakes of the corolline epidermis. In order to remove all possible doubt, it would of course be necessary to study the development of the fimbriæ.

In other exemplifications of the *Lophanthe* type the fimbriæ are *perinectarial*; that is to say, they are developed, not in longitudinal series parallel with and close to the stemono-petaline symphyses, but in close relation with the margins of the nectarial areæ.

The species in which I have met with the *Lophanthe* modification are:—

1. With *parastemonal* fimbriæ.

A.	B.	D.	E.
Gentiana	Gentiana	Gentiana	Gentiana
ciliata.	foliosa.	montana.	montana.
crinita.	rupicola.	diemensis.	concinna.
barbatula.	Hookeri.	pleurogynoides.	
	fastigiata.		
	cerastioides.		
	cernua.		
	Jamesonii.		
	radicata.		
	limoselloides.		
	diffusa.		

2. With *perinectarial* fimbriæ.

Swertia (Ophelia).
Frasera.

The fimbriæ of *Swertia* and *Frasera* are well known. In the *Gentianæ* proper the only distinct account of them which I have met with is that given by Müller ('Alpenblumen,' p. 343, *G. ciliata*). The disposition of the fimbriæ in the various species in

which they occur is well worthy of a more careful and detailed study than it has yet received. In some species (e.g. *Gentiana montana*, *pleurogynoides*, and *rupicola*) the parastemonal fimbriæ are so minute as to suggest that they may be absent in some varieties, which would thus effect a transition between *Lophanthe* and *Actinanthe*. Sir J. Hooker ('Flora of New Zealand') has already suggested that *G. concinna*, *saxosa*, and *pleurogynoides* may be varieties of *G. montana*. Perhaps it may be as well to mention that the mycelia of fungi, not infrequent in dried flowers, occasionally resemble fimbriæ.

IV. *Stephananthe.*

The corolla is elongated, campanulate, or infundibulate; the relatively short lobes becoming deflexed at right angles to the elongated "cup" in the fully expanded flower. Just below the junction of each lobe with the cup, the inner wall of the corolla is produced into a transverse ridge, the free, slightly convex, edge of which becomes divided into a number of broad flat unequal lobes, and these, again, subdivide into approximately equal, flat, elongated and pointed pectinations. The longitudinal axis of these (in the species which I have examined) is traversed by a vascular bundle derived from the veins of the corolla; and, in this respect, they differ from the fimbriæ of *Lophanthe*, in which I have found no vascular bundles. For the sake of distinguishing them from the fimbriæ, I propose to call these structures, which constitute the well-known "corona," *pectines*.

It is easy to imagine that the *pectines* may have been derived from parastemonal fimbriæ, by the transverse extension of the upper ends of the two series of such fimbriæ until they met in the middle line, while the longitudinal part of each series became aborted; but I have met with no indication of the transitional forms between *Lophanthe* and *Stephananthe* which, on this hypothesis, must have existed. In *Frasera* there are transversely disposed rows of fimbriæ which have a certain, though not very close, resemblance to the pectines; but they are situated on the basal side of the nectaries and close to them, while the pectines are on the opposite side and far away from the nectaries. In the expanded flower, the pectines are directed upwards and inwards, sometimes more in the one direction, sometimes more in the other. It would be very interesting to ascertain whether their position

does, or does not, vary according to the state of development of the pollen and the stigmatic surfaces.

The following species are referable to this type. Those marked with an asterisk are placed here on the authority of Grisebach or of Weddell.

A.	B.
Gentiana	Gentiana
Amarella.	liniflora.
campestris.	nitida.
germanica.	*inflata.
tenella.	*thyrsoidea.
*auriculata.	*crassolæma.
*nana.	*trichostemma.
*livonica.	*scopulosa.
*acuta.	*filamentosa.
*floribunda.	*Ringii.
*mexicana.	

These are all the types of floral structure which I have met with in the Perimelitous series. It will be observed that, looking at them broadly, they present a general progress, so far, as the shape of the corolla is concerned, from the stellate form with deeply divided lobes in, e. g., *G. aurea*, to the infundibulate form with sharply deflexed lobes in, e. g., *G. campestris*; and so far as the difficulty of access to the nectaries is concerned, from the openness to all comers in the first case, to the hiding away at the end of horns in *Keratanthe*, the partial barring of the road in *Lophanthe*, and the more complete obstruction offered by the corona in *Stephananthe*.

In the series of the *Mesomelitæ* the following modifications have presented themselves:—

V. *Asteranthe.*

The corolla is rotate, the cup being very short and the lobes very long. There are no plicæ, fimbriæ, or other appendages, and the expanded flower is widely open.

I find this structure only in the genus *Eustoma* and in *Gentiana lutea.* I am unable to say anything definite about the nectarial surfaces in the former, except that there are none discoverable on the corolla. In the latter, they are well known to form a zone round the base of the ovary. Neither *Eustoma* nor *Gentiana lutea* are, theoretically speaking, satisfactory representatives of the least modified forms of the Mesomelitous series.

For this purpose a Gentian with a flower like that of *G. saxosa*, but with the nectaries ovarian, is wanted; and I have not been able to find any which fulfils this requirement. In *Eustona* the calyx and the ovary are specialized in the direction of the type which I shall describe under the head of *Lissanthe*; and in *Gentiana lutea* in the direction of *Ptychanthe*. The spathose calyx and the ovary of *Gentiana lutea* present points of strong resemblance to those of *G. purpurea*; and the free hybridization, under natural conditions, of the two last-mentioned species is asserted upon apparently strong evidence. In my opinion, however, that evidence is by no means so conclusive as it looks at first sight; and the facts of the case require careful and experimental re-examination.

It is of course possible that *G. lutea* may be an ally of *G. purpurea* which has reverted to a less modified condition; but at present I see no sufficient grounds for adopting that hypothesis.

VI. *Limnanthe*.

The corolla is rotate and devoid of nectaries. The margins of the lobes may be laciniated; or their surfaces may be beset with longitudinal rows of fimbriæ (*Menyanthes*). Five, apparently glandular "hypogynous" tubercles are commonly developed at the junction of the walls of the ovary with the perianthial cup, which is more or less adherent to the base of the ovary.

A.	B.	C.
Menyanthes. Limnanthemum.	Limnanthemum.	Limnanthemum. Villarsia.
D.		E.
Liparophyllum. Limnanthemum. Villarsia.		Liparophyllum.

All systematic botanists recognize the aberrant character of the *Menyantheæ*. But I do not find in the works which I have consulted any notice of the circumstance that some of them, at any rate, present a more or less marked perigyny. I have examined only *Limnanthemum indicum, Menyanthes trifoliata, Villarsia capensis*, and *Liparophyllum Gunnii*; but in all these the perianth adheres to the base of the ovary, and the adhesion becomes more and more extensive in the order in which the species have been named.

VII. *Lissanthe.*

The corolla is devoid of nectaries. Sometimes there are distinct, apparently nectarial, tubercles on the base of the ovary; but, in the great majority, the presence or absence of nectarial surfaces has yet to be determined. Many are said to have "rotate" corollæ; but in all such which have come under my observation the corollæ are really hypocrateriform. Usually, the corolla varies from campanulate to long-tubed infundibulate forms; and the cup or tube is thin-walled, elastic, and pretty closely embraces the ovary. The filaments are inserted, sometimes very low down, and sometimes very high up in the tube. In some cases the anthers are united round the style, and the stigmas form a circular disk above the synantherous staminal ring (*Voyria*).

α. Corollæ short-tubed (hypocrateriform).

Lapithea, Exacum, Chironia, Sabbatia, Dejanira.

β. Corollæ long-tubed (infundibulate).

Chlora, Erythræa, Canscora, Coutoubea, Prepusa, Lisianthus, Tachiadenus. Belmontia, Voyria.

Here, as in preceding cases, the principle of the observed modification is obviously the interposition of obstacles in the way of access to the deep-seated portions of the cavity of the flower. In this respect, the flowers of *Voyria* and those of the long-tubed *Lisianthus* and *Tachiadenus* are models of obstructiveness.

I have examined species of the following genera:

A.	B.	C.	D.	E.
Erythræa.	Erythræa	Erythræa	Erythræa.	Erythræa.
Chlora.				
Sabbatia.	Sabbatia.	Exacum.		
	Dejanira.	Sebæa.	Sebæa.	Sebæa.
	Coutoubea.	Belmontia.		
	Prepusa.	Tachiadenus.		
	Tachia.	Chironia.		
	Lisianthus.	Canscora.	Canscora.	
	Voyria.			

The nature of the cup-like "hypogynous disk" of some of the "Lisyantheæ" of Grisebach requires investigation. In the only species presenting this structure which I have examined, it appears to be formed by the coalescence of expansions of the bases of the filaments.

VIII. *Ptychanthe.*

The corolla is campanulate or infundibulate, never rotate. The wall of the tube, between the interlobular sinuses and the insertion of the filaments, is produced into a series of longitudinal plications or "interlobes," the folded edges of which project into the throat of the tube, and more or less completely divide it into a corresponding number of longitudinal passages. The free margins of the interlobes may extend as far as those of the lobes, and they may be provided with long laciniæ. In some species the anthers cohere into a ring round the style, below the stigma, which last may take the form of a disk. Very often, the stemono-corolline symphyses are produced into strong longitudinal ridges, which continue the direction of the interlobular folds, and, by abutting against the ovary, subdivide the basal moiety of the cavity of the flower into passages which continue those in its marginal half. The base of the ovary is often tuberculate and clearly nectarigenous. The basal portion of its cavity is often devoid of ovules; and, sometimes, is elongated into a narrow stipes, which, in certain cases (e.g. *Crawfurdia*), attains a great length.

This type of structure is found exclusively in those species of the genus *Gentiana* which are included by Grisebach under the heads of *Cœlanthe*, *Tretorhiza*, *Cyane*, *Chondrophyllum*, *Thylacites*; in some of the *Andicola*; and in the genus *Crawfurdia*.

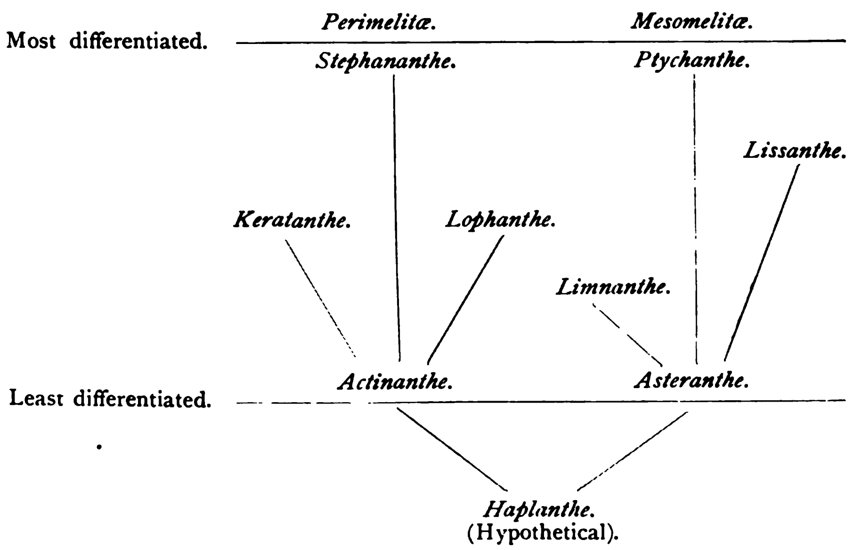
I have specially examined the following out of the numerous species which exhibit this type of structure, several in the fresh state:—

A.	B.	C.
Gentiana	Gentiana	Gentiana
verna.	sedifolia.	pedicellata.
prostrata.	prostrata.	zeylanica.
squarrosa.	spathacea.	Loureirii.
asclepiadea.	adsurgens.	
Andrewsii.	ramosissima.	
affinis.	Gayi.	
acaulis.		
purpurea.		
Burseri.		
punctata.		
cruciata.		
nikoensis.		
Buergeri.		
Thunbergii.		
japonica.		
Crawfurdia.		

Such are the types or leading modifications of floral structure which I have met with; and such the evidence, taken together with the extant descriptions of the forms I have not examined personally, on which I base the conclusion that they embrace all the most important morphological modifications of the corolla which the Gentianeæ offer. It will be observed that, unfortunately, they do not exhibit any particular relation to the received family, or even generic, groups. The accepted genus *Gentiana*, for example, exhibits no fewer than five of the eight types of floral structure; while the *Lissanthe* type is exhibited by some five-and-thirty accepted "genera." If *Frasera* and *Swertia* are to be regarded as generically distinct from *Gentiana*, I fail to see on what principle *G. amarella* and *G. purpurea*, which differ at least as much from one another as *Swertia*, *Frasera*, and *Gentiana* do, can be grouped into one genus. Considerations of this kind, which might be multiplied indefinitely, obviously suggest a thorough revision of the taxonomy of the Order—a task which I certainly shall not presume to attempt, but which will, I hope, be executed by some one more fitted to take such a large and difficult piece of work in hand.

Another important conclusion, which is naturally suggested by the facts to which I have drawn attention, is that the several types in each of the two series bear a certain progressive relation to one another. It is obvious that *Actinanthe* and *Asteranthe* are the simplest and least modified forms in each series; that *Stephananthe* is the most differentiated of the *Perimelitæ*; that *Ptychanthe* and the more specialized forms of *Lissanthe* are the most differentiated of the *Mesomelitæ*; while *Lophanthe* and *Keratanthe* in the one series, *Limnanthe* in the other, constitute lower grades of differentiation, though they are nowise to be regarded as transitional between any of the others.

Thus, on purely morphological grounds and as a mere generalisation of the facts, without the introduction of any speculative considerations, the relations of the various types may be represented thus:—



Or, to put the facts in another way, the several types in each series may be regarded as modifications of a common plan, of which the simplest exemplification is to be found in *Actinanthe* and *Asteranthe* respectively. If so, it is an easy step to the conclusion that both these are slightly diverse modifications of a still more simple, but, at present, purely hypothetical, common form, having the main features of *Actinanthe* and *Asteranthe*, but with the nectarial surfaces either feebly developed on both ovarian and corolline surfaces, or entirely absent. I will call this hypothetical " Ur-gentian," *Haplanthe.*

Thus far I have endeavoured to travel no hair's breadth beyond matters of observation and their obvious relations. It is plain that, even if all the five hundred and odd species of Gentianeæ had been created separately and raised in pots in the Garden of Eden, their morphological relations would have been exactly what they are.

But, to a believer in evolution, the significance of these facts is unmistakable. With whatever caution one may be inclined to regard phylogenic speculations, it is hard, in such a case as this, to resist the force of the suggestion, that these morphological relations do really indicate the path which the evolution of the plants composing the Order has followed. At any rate, the evidence is strong enough to justify us in accepting this conception as a good working hypothesis. And there is the more justification

for doing so, that, if we regard the morphological facts by the light of Sprengel and Darwin's theory of the origin of flowers, they at once become intelligible.

In foraging for information about the Gentians, immediately after my return to England, I took up Müller's 'Alpenblumen'; and I was exceedingly struck by the views put forward in the remarkable page and a quarter which he devotes to a "Rückblick auf die Gentianarten" (p. 348), and which I here translate:—

"The genus *Gentiana* is fitter than almost any other to furnish a biological explanation, from the arrangements in regard to fertilization, of the systematic grouping based on morphological indications; and to dispose the subdivisions of the system as branches of a parent stem. It is primarily divisible into two main branches, of which the one secretes honey from the lowest part of the ovary, the other from the lowest part of the corolla. If, then, two kinds of nectarial structure have arisen from an original uniform nectarial structure, the common ancestor of these two groups must have secreted honey, both from the base of the ovary and from that of the corolla, as is the case, *e.g.*, in *Saxifraga oppositifolia*; and thus in the one group the one half, and in the other the other half, must have been specially developed, to the exclusion of its fellow. But it is also conceivable that the ancestors of *Gentiana* were honeyless, and that the two forms of nectary have been developed independently.

"Of the one of the two main branches, we have a lateral twig remaining in *G. lutea*, which stands low down in point of development, and is certainly nearest the common stem. Like *G. lutea*, without doubt, the ancestors of the genus had fully open flowers, with almost free petals, and tempted the appetite of their fertilizers, either with perfectly accessible honey, in the angle between the ovary and the corolla, or only with pollen. In any case, they were open to the visits of very various insects, which therefore subserved cross-fertilization irregularly and, as it were, accidentally (as in *G. lutea*), so that the occurrence of such fertilization was by no means assured, and spontaneous self-fertilization in case of need could not be dispensed with.

"After the development of the nectaries, Bees, and especially Humble-bees, proved the most effective cross-fertilizers; and campanulate flowers adapted to them became developed. In the one branch, unbidden guests were excluded by the formation of deep passages (*Saftlöcher*); and, by the coalescence of the anthers into a ring round the style, cross-fertilization by Humble-bees

was assured (*Cœlanthe*[1]). In the other branch, fimbriæ of the petals, at first, afforded an imperfect defence against useless visitors, and narrowing of the flower insured the contact of the Bees with the stigmas as well as with the anthers (*Crossopetalum*[2]).

"Subsequently, in the one main branch, under the conditions already indicated, the *Cœlanthe*-form, adapted to Humble-bees, was bred into the *Cyclostigma*-type,[3] adapted to Butterflies: whilst in a particular offshoot of the other main branch, the development of the pectines and the narrowing of the corolla around the ovary brought Butterflies as well as Humble-bees into service as cross-fertilizers (*Endotricha*[4]).

"The original yellow colour of the flowers (as in *G. lutea*) was gradually changed into blue by the selective action of Humble-bees; and instructive intermediate stages of this process are seen in the species of *Cœlanthe*. But after the blue coloration was once fixed, the colour maintained itself throughout the process by which Butterflies, by unconscious selection, bred *Cœlanthe* into *Cyclostigma*."[5]

I confess that, when I first read this uncompromising application of the theory of flowers, originated by Sprengel and Darwin, to the case of the Alpine Gentians, I thought it somewhat rash, and gave it a very cool and sceptical reception. It occurred to me that if it was a valid explanation of the morphological characters of the flowers at all, it ought to be applicable not only to those of the Alpine *Gentianæ*, but to the whole genus; and, if to the genus, then why not to the whole order? And the chief motive which has led me to spend a good deal of time and trouble in working over a considerable proportion of the species of *Gentiana* and of the genera of Gentianeæ, was the obvious importance of arriving at some conclusion respecting this question.

I do not profess to have settled it; but, so far as I have gone, I have found nothing that conflicts with Müller's extremely ingenious speculation. On the contrary, everything confirms it. As I have already remarked, the principle which underlies the

[1] *Ptychanthe* (mihi).
[2] *Lophanthe* (mihl).
[3] *Ptychanthe* (mihi).
[4] *Stephananthe* (mihi).
[5] Sir Joseph Hooker ('Flora of New Zealand') observes that the pure blue of the European and Himalayan Gentians is unknown in the Arctic regions and the higher latitudes of the Andes. The widespread *G. montana* has pale whitish-yellow flowers streaked with red or blue. These facts are interesting in relation to the primitive character of the Novo-Zelanian, Australian, and Austro-Columbian Gentians.

progressive modifications of the flower, in each of my series, is the gradual interposition of more and more obstacles in the way of easy access to the nectaries. Yet these obstacles, whether they arise out of a mere narrowing and elongation of the tube of the corolla, as in *Lissanthe*, or out of the development of fimbriæ and pectines (as in *Lophanthe* and *Stephananthe*), or of interlobes, synanthery, and discoidal stigmata (as in *Ptychanthe*), are always of such a nature that they afford no effectual hindrance to the passage of a thin and flexible organ, like the haustrum of a suctorial insect, but only just sufficient obstacle to make the insect an efficient agent in cross-fertilization.

Few inquiries would be more interesting and profitable (though undoubtedly few more difficult) than the working out of the geographical distribution of the Gentianeæ in relation to the Insect Faunæ of the several regions in which they occur.

I merely note that those Gentianeæ which have remarkably long infundibulate corollæ are found in regions, such as Madagascar and Guiana, which are tenanted by large Lepidoptera provided with long haustra.

Müller's doctrine respecting the origin of the forms of the flower in the Alpine *Gentianæ* appears to me to be equally applicable to the whole of the Order, and to supply a true cause whereby the morphological facts may be correlated and explained.

I do not suggest that the interaction of cross-fertilizing insects with the variation in the structure of the corolla accounts for all the characters by which the five hundred species of Gentianeæ differ from one another. Why one species is annual and another has a rhizome; why the great majority have opposite palmati-veined leaves, while some have alternate or pennati-veined leaves; why the majority have a single-celled ovary, and yet, in many, the ovary is more or less completely two-celled [1]; why most are herbaceous, while some are bushy and some are climbers, are problems hardly to be solved by the consideration of the causes which have brought about the modification of the corolla. But I have little doubt that, with

[1] The partially, or wholly, two-celled ovary appears to be generally regarded as the result of the gradual introrsion of the margins of the carpellary phyllomes into the cavity of a primitively one-celled ovary. But had *Haplanthe* a one-celled ovary? Must not the apocarpous condition precede the syncarpous? Does not the state of the ovary in Apocyneæ and Asclepiadeæ rather suggest that the primitive Gentians (or perhaps, I should rather say, the primitive stock of all these orders) had an ovary like that of a hypogynous Saxifrage?

larger knowledge, analogous causes will be found to be operative in all these cases. One of the great lessons which Darwin has taught us is faith in the doctrine of sufficient causes; and consequently hesitation in assuming that any structure, however slight or unimportant in appearance, is devoid of significance in relation to either present or past conditions of existence, the chiefest of these being the struggle for existence with competitors, while climate and station probably occupy a very secondary place.

Even in respect of geographical distribution—upon which climate and station are usually assumed to exercise so great an influence,—facts which have come under my notice in studying the Gentians have led me to be a little sceptical as to the extent of that influence.

At Arolla I never met with a specimen of *Gentiana acaulis* anywhere except in the region between the pine-woods and the snow-line. Yet this same species grows so freely in some parts of Southern England, as to be used for the borders of beds, in a kitchen-garden.[1] The genus *Erythræa*, which is notorious for the slightness of the differences between its "species," is of world-wide distribution. It occurs all over Europe, in the Sinaitic Desert, in Egypt, in Hindostan, in the hottest parts of Australia, and in the moist temperate climate of New Zealand. Mr. Gunn, in a note appended to specimens of *Gentiana montana* in the Kew Herbarium, says that this species occurs everywhere, from the shore to the summit of the mountains. *Gentiana campestris* is said by Hooker and Arnott to be "abundant in Scotland, especially near the sea." It was no less abundant at Arolla from 6,400 feet to the snow-line.

In studying, with some care, the geographical distribution of various large and widespread groups of closely allied animals, such as the *Canidæ*, the *Astacomorpha*, and freshwater Fishes, I have been much impressed by the necessity of a most minute study of their morphology as a preliminary to any attempt to deal with the facts of distribution. I think there is no greater mistake than to suppose that distribution, or indeed any other large biological question, can be studied to good purpose by those who lack either the opportunity or the inclination to go through what they are pleased to term the drudgery of exhaustive anatomical, embryological, and physiological preparation.

Elaborate works on Distribution have been published which

[1] Lady Elizabeth Cust informed me that this was the case at Cobham Park in her childhood.

are of little more value than catalogues of reference, because their authors have been unaware of this necessity. And I may point my remarks by showing that even such a brief and imperfect sketch of the minuter morphological characters of the Gentians as is here presented is fruitful of suggestions in regard to their Distribution.

My studies of Animal Distribution have led me to the belief that the division of the land-surface of the globe into large areas, which corresponds most nearly with the broader facts, may be stated as follows. Europe, Africa, Asia, and North America as far as Mexico form one great province—ARCTOGÆA ; in which Ultra-Saharal Africa, Madagascar, Hindostan, and Indo-China are more or less. distinctly characterized as subprovinces. For my present purpose it will suffice to speak collectively of the latter as the Southern Arctogæa, in contradistinction to the rest of the province as Northern Arctogæa. South America, with the Isthmus, as far as Mexico, constitutes a second great province, AUSTRO-COLUMBIA ; Australia with the adjacent islands a third ; while New Zealand and the neighbouring islets may be most conveniently regarded as a fourth.

In mentioning the species of the various types of Gentianeæ which I have examined, I have arranged them under the heads of A, for Northern ARCTOGÆA, B, AUSTRO-COLUMBIA ; C, Southern ARCTOGÆA ; D, AUSTRALASIA ; E, NOVO-ZELANIA

Adopting this scheme of four great distributional provinces. one of which is subdivided into two regions, the following propositions appear to me to hold good of the Gentianeæ :—

1. Species of the Order are found in all five regions. They flourish within the Arctic Circle and up to the limit of perpetual snow in mountain-ranges. They also abound in sundry tropical climates, both moist and dry. The *Limnanthe* type, represented exclusively by marsh- or water-plants, occurs in all the regions, and will not be further mentioned.

2. The head-quarters of the Order (if we consider the number of types represented) are in the North Arctogæal and the Austro-Columbian regions, both of which contain representatives of all the types.

3. The Australasian, South Arctogæal, and Novo-Zelanian regions are all poorer in types. South Arctogæa contains only three, *Lophanthe*, *Lissanthe*, and *Ptychanthe* ; Australasia two, *Lophanthe* and *Lissanthe* (perhaps *Actinanthe*) ; Novo-Zelania three, *Actinanthe*, *Lophanthe*, and *Lissanthe*.

4. The Australasian and Novo-Zelanian provinces have very few species; in the Northern and Southern Arctogæal regions they are very much more numerous. Their numbers are greatest in Austro-Columbia.

5. Only one species is certainly known to be common to any large extent of two provinces, namely *Gentiana prostrata*, which extends from the Eastern Alps of Europe, by way of Northern Asia and America, to the southern extremity of South America.

6. The only types which certainly occur in all five regions are *Lophanthe*, *Limnanthe*, and *Lissanthe*. *Actinanthe* is known in three; namely, the Northern Arctogæal, the Austro-Columbian, and the Novo-Zelanian. I think it probable, however, that it may yet be found in Australia. *Keratanthe* and *Stephananthe* occur in two, Northern Arctogæa and Austro-Columbia; *Ptychanthe* in three, Northern and Southern Arctogæa and Austro-Columbia.

7. Notwithstanding the general similarity of the climatal conditions in the mountain chains of Northern Arctogæa and Austro-Columbia, and the abundance of Gentians in both, their Gentian Floræ are fundamentally different. In the Pyrenees, the Alps, and the Himalayas, the *Ptychanthe* type is largely represented in relation to the *Actinanthe*, *Lophanthe*, and *Stephananthe* types.

In the Andes it is just the other way. Gentians of the *Actinanthe* and *Lophanthe* types abound, and *Stephananthe* is well represented; while I cannot make sure of more than six representatives of *Ptychanthe*, though this type is so easily recognized that there is little chance of its being overlooked or mistaken. Out of more than 60 species of South-American *Gentianæ*, enumerated in Grisebach's 'Genera' and Weddell's 'Chloris,' it appears that nine, namely, *G. nitida*, *liniflora*, *inflata*, *thyrsoidea*, *crossolæma trichostemma*, *scopulosa*, *filamentosa*, and *Ringii*, belong to *Stephananthe*, and six to *Ptychanthe*; while the rest all belong either to *Actinanthe* or to *Lophanthe*. Judging from the proportion of those which I have examined, it seems probable that there are nearly as many of *Lophanthe* as of *Actinanthe*.

And when it is considered that only one species is common to the highlands of Northern Arctogæa and of Austro-Columbia, the contrast between the Gentian Floræ of the two becomes still more striking.

In Sir Joseph Hooker's well-known paper "On the Distribution of Arctic Plants" ('Transactions Linn. Society,' vol. xxiii.), the following twelve Gentianeæ are stated to occur north of the

Arctic Circle:—*Gentiana aurea, propinqua, detonsa, arctophila, Amarella, tenella, glauca, prostrata, nivalis, verna*; *Pleurogyne rotata, Menyanthes trifoliata.*

I have not examined *Gentiana arctophila*; but I believe it to belong, like *G. aurea, propinqua,* and *detonsa,* to the *Actinanthe* type. In this case the components of the Gentian Flora of the Arctic regions may be classified as follows:—

Actinanthe.	Keratanthe.	Lophanthe.	Stephananthe.
5	0	0	2
Limnanthe.	Asteranthe.	Lissanthe.	Ptychanthe.
1	0	0	4

In the Flora of the European Alps I can find no representative of the *Actinanthe* type except *Pleurogyne carinthiaca.* On the other hand, two of its Gentianeæ, *Gentiana ciliata* and *Swertia perennis,* belong to *Lophanthe.*

Passing to the *Stephananthe* type, *Gentiana tenella* is admittedly common to the Alps and the Arctic regions; but the former have *G. germanica, campestris,* and *nana* in place of *G. amarella.* How far any real distinction is to be drawn between *G. amarella* and *G. germanica* is a question for future examination.

Limnanthe is represented by *Menyanthes trifoliata* in both the Arctic and the Alpine regions; *Asteranthe* only in the Alpine; *Lissanthe* in neither.

The ordinarily recognized species of *Ptychanthe* in the proper Alpine region of Europe are some eighteen or nineteen in number. Three of these, namely, *G. verna, nivalis,* and *prostrata,* are also Arctic; but the Gentians of the *acaulis* group, which flourish along with *verna* and *nivalis* in the Alps are unknown in the Arctic regions. Again, the Gentians of the *purpurea* group, though they occur in Southern Scandinavia and Kamtschatka, stop short of the Arctic Circle.

It appears to me that these facts are very difficult to reconcile with the view that the high Alps have been peopled with their Gentianeæ from the Arctic regions or *vice versa.* The abundance of Gentians of the *Actinanthe* type in the Andes indicates their adaptability to alpine conditions; yet they are absent in the Alps, while well represented in the Arctic regions.

It must be understood that I deal only with the broad facts of the case. Some attempts which I made to study the few forms which abounded at Arolla, with a view of distinguishing the book-species among them, became unsuccessful exactly in pro-

portion to the number of specimens I examined ; and I left off with the conviction that I had no means of knowing whether *G. purpurea* was distinct from *G. punctata*, *G. campestris* from *G. germanica*, or *G. verna* from three or four other "species." In *G. campestris* the number of varieties in size, habit, foliation form, number of parts and colour of the flower, were really astonishing; and I met with the strangest monstrosities. In *G. verna* the range of variation was quite as remarkable. If all the species of *Gentianæ* are in this case, it is perilous to attempt numerical estimates on the foundation of ordinary collections.

DISTRIBUTIONAL DIAGRAM.

NORTH ARCTOGÆA.
Actinanthe.
Keratanthe.
Lophanthe.
Stephananthe.
Asteranthe.
Limnanthe.
Lissanthe.
Ptychanthe.

AUSTRO-COLUMBIA.	SOUTH ARCTOGÆA.	AUSTRALASIA.	NOVO-ZELANIA.
Actinanthe.	. . . . .	(?)	Actinanthe.
Keratanthe.	. . . . .	. . . . .	. . . . .
Lophanthe.	Lophanthe.	Lophanthe.	Lophanthe.
Stephananthe.	. . . . .	. . . . .	. . . . .
Asteranthe.	. . . . .	. . . . .	. . . . .
Limnanthe.	Limnanthe.	Limnanthe.	Limnanthe.
Lissanthe.	**Lissanthe.**	Lissanthe.	Lissanthe.
Ptychanthe.	Ptychanthe.	. . . . .	. . . .

The names printed in black letters are those of strongly dominant types in the several regions.

If the facts of distribution of the Gentianeæ are adequately stated in the above propositions, one conclusion appears to me to be very clear; and that is, that they are not to be accounted for by migration from any "centre of diffusion," to which a locality can be assigned in the present condition of the world. If the *Gentianæ* of the Andean range had been derived from those of Northern Arctogæa or *vice versa*, it seems unaccountable that the proportion of representatives of the types should be so different in the two assemblages ; and, still more, that there should be only one species common to both.

There is a well-known case of zoological distribution which presents a certain parallelism with that of the *Gentianæ*. The

genus *Tapirus* is represented by certain species in South America, and by another in the Indo-Malayan region. And palæontology furnishes the explanation of the fact by proving the existence of Tapirine animals, which have since died out, over the vast intermediate area in the Middle Tertiary epoch. There has been no migration, but simply local modification of the genus at opposite ends of its primitively continuous area of distribution, with subsequent extirpation over the intermediate space.

I am not aware that any fossil remains of Gentianeæ have been brought to light; but it is known that many of the plants of the Middle Tertiary epoch were extremely similar to those which now exist. Furthermore, it is certain that the great elevated areas of both the Old and the New Worlds existed, and had attained a considerable height, possibly even greater than that which they at present possess, during the Pliocene epoch. Under these circumstances, I see no reason to object to the supposition that species of the genus *Gentiana* itself, closely similar to our existing species, may have, at that time, occupied pretty much the same regions and stations as those in which they are now found, and had already adjusted themselves to their hard conditions of existence. If so, the changes in the physical geography of the world, which preceded and accompanied the Glacial Epoch, must undoubtedly have narrowed the range, and probably extirpated a good many of the pre-Glacial species of *Gentiana*. But the remainder would have as readily found secure refuge in sheltered nooks and valleys, as the existing species do; and, as the climate improved with the passing away of the Glacial epoch, they would start afresh from their fastnesses to compete with other immigrants for the possession of the new localities laid open to them.

Gentiana prostrata may have had its present distribution before the Glacial epoch. In fact, I am more surprised to find only one species widely spread over both the Northern Arctogæal and the Austro-Columbian provinces, than I should be if there were several; and I am not a little disposed to think that a serious critical comparison of the two Floræ, with due attention to the range of variation of the species in each, may bring about a considerable alteration of our views on this subject.

The supposition that the distribution of the Gentianeæ in Pliocene or in Miocene times was substantially similar to what it is now, is of course no solution of the problem of their distribution; it is simply driving the search for that solution further back. Is it possible to fix any anterior limit to this retrogression?

I suppose it would be, if one could fix the age of the first appearance of Diptera, Hymenoptera, and Lepidoptera provided with long haustra. For, upon Müller's hypothesis, the existence of the *Keratanthe*, *Stephananthe*, *Lissanthe*, and *Ptychanthe* types presupposes that of such insects. Unfortunately, we are, as yet, hardly in a position to speak positively on this point. The most that can be said is that there is no evidence that they were abundant before the middle of the Mesozoic epoch, or that they existed in Palæozoic times. Free play, therefore, is left to speculation; and I do not think any good grounds could be given for denying the existence of even the more specialized Gentianeæ in the Cretaceous epoch; while the "Ur-Gentian," the hypothetical anemophilous *Haplanthe*, may be dated back almost as much further as probabilities permit us to carry the existence of flowering plants. For it is obvious that a very slight further modification, in the direction of simplicity in *Haplanthe*, would bring about a form of flower which might serve as the starting-point for those of almost all the Orders of Dicotyledons. But speculation as to when or where the hypothetical *Haplanthe* may have originated is, for the present, idle. "Ignoramus" and, I fear, for a long while "ignorabimus."

Considering how slight the morphological differences between the eight types really are, and that (according to the hypothesis) they have been brought about by the selective operation of agencies of the same order, it seems to me that it would be rash to deny that species belonging to the same type may have arisen in different localities. I do not think it probable that the process of modification and the materials it works upon would be so similar in widely different localities as to give rise to the close similarities which lead us to group individuals in the same species; but the polygeny of genera, and still more of larger groups, appears to me to be highly probable.[1]

We are very much in the habit of tacitly assuming that because certain plants and certain animals exist only under certain climatal conditions, there is something in what we vaguely call the "constitution" of the plants or animals which binds them to these conditions, and renders it impossible for them to live elsewhere. I wish we could get rid of this word "constitution"; for I take it to be one of the many verbal anodynes by which the discomfort of ignorance is dulled. If it means anything definite,

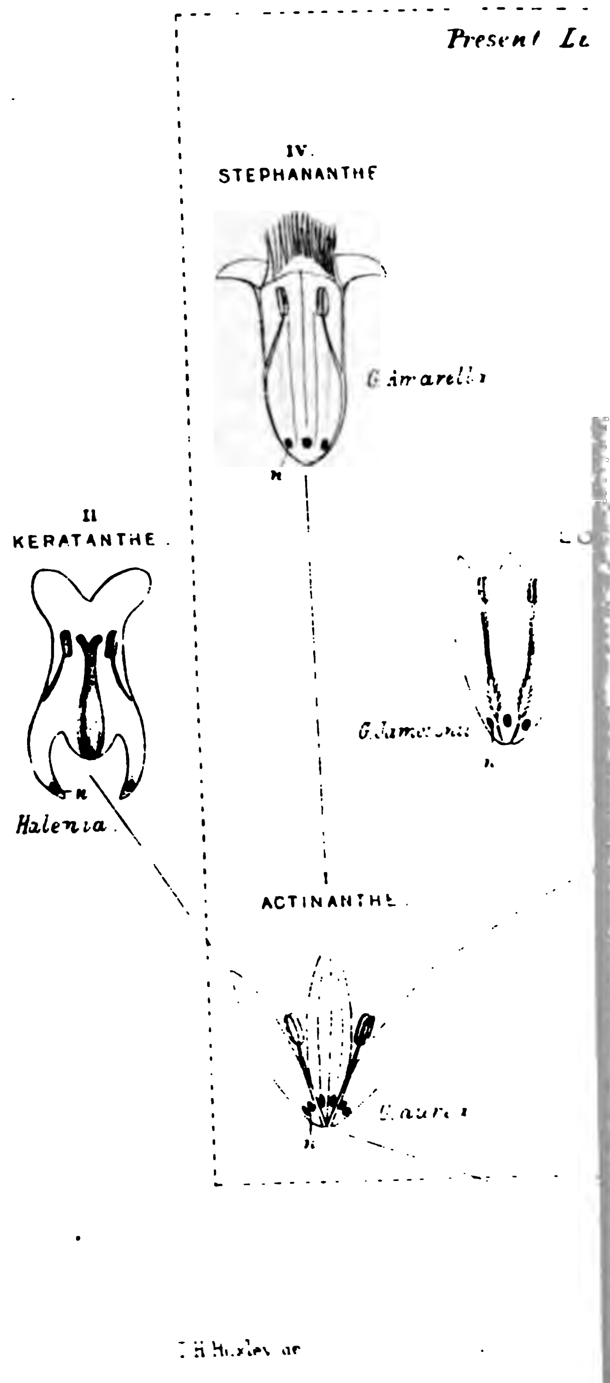
[1] I find weighty remarks on this topic in Engler's 'Versuch einer Entwickelungsgeschichte der Pflanzenwelt,' 2 Theil, p. 318.

it merely signifies that there is some morphological or physiological impediment to the existence of the plant or animal, outside the defined conditions; and our business is to find out what that impediment is. When I was at Arolla I was extremely astonished by the distribution of two very common species of *Epilobium* (*E. spicatum* and *E. Fleischeri*), which were flowering at the same time. There was any quantity of the latter among the boulders of the bed of the stream at the bottom of the valley; but nowhere else. And there was any quantity of *E. spicatum* growing on the lateral walls of the valley, from 30 or 40 feet above its bed upwards, but nowhere else. I used to amuse myself by looking for trespassers of either species in the province of the other; but I never could find any. Everybody knows that the seeds of the *Epilobia* are abundant and provided with special aids to distribution by the winds; and there certainly is no failure of breezes in the valley. Every year, therefore, millions of seeds of each species must be scattered over the territory of the other. Why does one thrive, and the other die?

To say this depends on the "constitution" of the two species, is simply to wrap up the fact in another form of words. And I can conceive of no investigation more likely to lead to results of far-reaching importance, than that which should get to the bottom of this, or any analogous case.

Finally, I may put another question. Is anybody in a position to deny that, in the absence of all other phænogamous vegetation, the Gentians might have occupied every region and station on the earth's surface in which flowering plants can exist? Is there any ground for seeking the causes of their distribution elsewhere than in the composition with other plants which they have undergone and are undergoing, and in the course of which it has often happened that the success of a given form in adapting itself to certain conditions has involved a corresponding diminution of the faculty of adapting itself to others?

Such are the observations I have to offer. I call them "Notes and Queries;" and I am afraid there are more queries than notes. My hope in offering them to the Society is to stimulate those who are better qualified than I am to carry through a serious botanical inquiry, and who have more time before them than I have to take up the subject. I believe that the systematic and exhaustive study of a single well-chosen Order, and of all the biological problems which it presents, would


Present Le
IV.
STEPHANANTHE
G. Amarella
II
KERATANTHE.
Halenia.
G. Jameson
I
ACTINANTHE.
G. aurea
T. H. Huxley del.

inaugurate a new era in the progress of Botany. The amount of patient and sagaciously directed labour which is embodied in our standard systematic works is astounding; and the deepest gratitude is due to those who have thus brought the data of Vegetable Morphology and Distribution into a shape in which they can be dealt with. But from the point of view of the Evolution doctrine, it is obvious that Taxonomy and Distribution have to be subjected to a process of revision, which will hardly fail to revolutionize both.

DESCRIPTION OF PLATE II. [PLATE 26].

A scheme to illustrate the morphology of the flower of the Gentianeæ.

XXXVII

FURTHER OBSERVATIONS UPON HYPERODAPEDON GORDONI.

The Quarterly Journal of the Geological Society of London, vol. xliii., 1887, *pp.* 675-694. (*Read May* 11*th*, 1887.)

(PLATES XXVI. AND XXVII. [PLATES 27, 28].)

IT is now twenty-nine years since, in describing those remains of *Stagonolepis Robertsoni* from the Elgin Sandstones which enabled me to determine the reptilian nature and the crocodilian affinities of that supposed fish, I indicated the occurrence in the same beds of a Lacertilian reptile, to which I gave the name of *Hyperodapedon Gordoni.* I laid stress upon the "marked affinity with certain Triassic reptiles" (e.g. *Rhynchosaurus*) of *Hyperodapedon*, and I said that these, "when taken together with the resemblance of *Stagonolepis* to Mesozoic Crocodilia," led me "to require the strongest stratigraphical proof before admitting the Palæozoic age of the beds in which it occurs." [1]

Many Fellows of the Society will remember the prolonged discussions which took place, in the course of the ensuing ten or twelve years, before the Mesozoic age of the reptiliferous sandstones of Elgin was universally admitted. *Hyperodapedon* was destined to play no inconsiderable part in the controversy. Some ten years after the discovery of the original specimen, remains referable to the same genus were found in strata of unquestionably Triassic age in Central and Southern England ; and, about the same time, I received abundant evidence of the occurrence of *Hyperodapedon*, associated with Dicynodonts, Crocodilia, and Labyrinthodonts, in certain Indian rocks

[1] Quart. Journ. Geol. Soc. vol. xv. 1859, p. 460.

which, on other grounds, were strongly suspected to belong to the oldest Mesozoic series. An account of these new materials, together with a full description of the original specimen of *Hyperodapedon*, was read before the Society and published in the 'Quarterly Journal' for 1869.[1]

Unfortunately the type specimen, now in the Elgin Museum, was in very bad condition; and though, by careful study of the fossil itself, it was possible to make out all the most important features of the skeleton, the work of the artist employed to figure it turned out so unsatisfactory, that I abstained from publishing the two plates which were prepared for the Memoirs of the Geological Survey, thinking it wiser to wait until better materials should make their appearance. My discretion has been justified by the event, as a second specimen, of almost exactly the same dimensions as the first, was discovered in the Lossiemouth Quarries, and became the property of the British Museum some time ago. It has been worked out with a skill which my old experience of the nature of the matrix of these Elgin fossils enables me fully to appreciate, by Mr. Hall, and my friend Dr. Woodward has been so good as to place it in my hands for description.

I am glad to be able to say that, so far as it goes, the account of the structure of the skeleton of *Hyperodapedon* which I gave in 1869 needs no correction; but the new material enables me to make large and important additions. Moreover, several specimens of *Rhynchosaurus articeps* in the Palæontological Collection of the British Museum render it possible to make a full comparison of *Rhynchosaurus* with *Hyperodapedon*, and to put an end to any doubts which may have been entertained as to the generic distinction of the two. Finally, the full evidence now accessible permits us to obtain a clear view of the relations of both these extinct genera with the recent *Sphenodon*, a point to which I drew particular attention in 1869.[2] These relations, both of resemblance and of difference, are so interesting and important, in fact, that I shall give my account of *Hyperodapedon* mainly in the form of a comparison between that genus and *Sphenodon*.

The present specimen of *Hyperodapedon Gordoni* has been exposed by the splitting of a large block of sandstone into two slabs, along a plane which corresponds roughly with that of the embedded skeleton. I have no information respecting the relative position of these slabs in the rock before it was quarried; but, supposing that slab which

[1] "On *Hyperodapedon*," Quart. Journ. Geol. Soc. 1869, vol. xxv. p. 138.

[2] *Loc. cit.* p. 147.

contains the larger part of the skeleton and the entire skull to have been uppermost, the animal lay flat upon its belly with its limbs standing out, very much as those of a dead Lizard ordinarily do, when it was buried in the sands of the Elgin shore. The skull, the vertebral column as far as the root of the tail, slightly curved towards the right side, almost the whole of the bones of the left (and part of the right) fore limb, with those of the right hind limb, are preserved in almost their natural relations.

The following table gives a view of the actual dimensions of *Hyperodapedon* and of the proportions of its parts compared with a specimen of *Sphenodon*:—

Measurements, in millimetres.

	Hyperodapedon.	*Sphenodon.*
Total length	(Probably over 2000)	460
End of premaxilla to end of second sacral vertebra ...	900	208 = (4·5 : 1)
Skull, end of premaxilla to edge of occiput	160	55 = (3 : 1)
Skull, greatest breadth of the occipital region	210	34 = (7 : 1)
Total length of humerus + radius	210	56 = (4 : 1)
Total length of femur + tibia.....................................	200	66 = (3 : 1)

Supposing the tail of *Hyperodapedon* to have been as long in proportion as that of *Sphenodon*, this specimen will have had a length of between six and seven feet, or rather more than four times as long as the specimen of *Sphenodon*. Hence it would appear that the skull and the hind limbs were relatively shorter in the extinct reptile, but otherwise it must have had much the general aspect of its New-Zealand ally—only, as I shall have occasion to point out more fully by and by, the skull was relatively much broader and more massive and the feet were shorter and stouter in *Hyperodapedon*.

There are certainly 23 præsacral vertebræ in *Hyperodapedon*, perhaps 24, but I think not more; *Sphenodon* has 25. In both genera there are two sacral vertebræ.

In the first specimen, such of the thoraco-lumbar vertebræ as were preserved were split through the middle vertically and longitudinally. The sections of the centra showed that they were well-ossified throughout, and they appeared to be terminated by slightly concave contours. In the present specimen, the ventral faces of the cervical, and of some of the anterior thoracic, vertebræ are exposed and are almost uninjured; but from that which I reckon to be the 13th (though it may be the 14th) to the 20th, they are split horizontally and longitudinally, the dorsal halves lying in the upper slab and the

ventral halves in the lower. The 21st, 22nd, and 23rd are similarly split, but they are much injured. Now the ends of several of these centra, notably the 13th, 14th, 18th, and 20th, present a sectional contour, which in front is more or less convex; while behind it is similarly concave. The anterior ends of the centra of the 4th (cervical) vertebra and of the 10th and 11th (thoracic) vertebræ appear to be strongly convex from side to side and their posterior faces correspondingly concave. Combining these appearances with those seen in the longitudinal section, I can only suppose that the surfaces must have been slightly cylindroidal, convex from side to side in front, and concave in the same direction behind; and thus that they approximated, though very distantly, to those of ordinary birds.

The remains of the slightly displaced atlas (Plate XXVI. [Plate 27] fig. 7) are seen immediately behind the skull. It has the form of a ring 26 millim. wide and 20 millim. in vertical height. Traces of the os odontoideum are visible immediately in front of the ventral portion of the ring, which lies horizontally, with its ventral region turned backwards. The front half of the second cervical vertebra is broken away, but its centrum appears to have been about 20 millim. long. The ventral faces of the third and fourth are well displayed. Each is about 20 millim. long and 17 millim. wide at the ends, but not more than 13 millim. at the middle. On each side of the anterior end a short broad tubercle, which represents the transverse process, is developed. I can find no indication of the existence of intercentral ossifications. Each vertebra possesses a pair of strong ribs (Plate XXVI. [Plate 27] fig. 8). These lie at the sides of the centra of the vertebræ and parallel with their length; so that, at first sight, the cervical region has a crocodilian look. The first rib on the right side is well seen. It is a straight styliform bone, 40 millim. long and 3 millim. wide. On its dorsal side, and more or less hidden by it, lies the second rib, the remains of which have about the same width and length. However, neither of these ribs is complete at its extremities. The right rib of the third cervical vertebra is 38 millim. long and 10 millim. wide at its head, but it gradually tapers to a point at its ventral end. The fourth cervical vertebra has a rib of similar dimensions, but curved somewhat in the shape of an italic *f*. This great development of all the anterior cervical ribs is a point of contrast between *Hyperodapedon* and *Sphenodon*, in which last only rudiments of such ribs are discoverable.

The fifth cervical vertebra is almost completely hidden under the shoulder-girdle, behind which a vertebra makes its appearance, which

I take to be the 9th, though it may be the 10th. The centrum of this vertebra is 20 millim. long, 25 millim. wide between the ends of the transverse processes in front, and 17 millim. wide in the middle of its length; and the centra of the three vertebræ which follow it have similar dimensions and appear to have concave posterior faces. These vertebræ have strong but short transverse processes. That of the 11th vertebra, on the right side, shows a rounded surface for the articulation of the head of the rib. The vertebral end of this rib is also well displayed; it is broad, measuring 20 millim. from its dorsal to its ventral margin, which is concave and thick, while the dorsal margin is thinner and convex (Plate XXVI. [Plate 27] fig. 9). The vertebral end of a similar rib is visible on the right side, close to the 16th vertebra, and there are less well-preserved remains of others. These ribs are very similar to the corresponding ribs of *Sphenodon*.

Nearly the whole length of the rib which belongs to the 12th or 13th vertebra is shown; it is about 12 millim. broad, flattened and truncated at the sternal end; it measures 153 millim. along the chord of the arc of its curvature. The vertebral end is not completely exposed.

A thin flat plate of bone, 20 millim. long by 14 millim. wide, is seen on the right side, overlying the remains of two vertebral ribs, opposite the 14th vertebra. I suspect that this is a "processus uncinatus," such as those which occur in *Sphenodon*. The position of the skeleton is unfavourable for showing such bones, if they were preserved, and they would readily become detached. Portions of eight ribs, in undisturbed series, corresponding to the vertebræ from the 18th to the 22nd inclusively, are seen on the right side. It is possible that these may be the ends of vertebral ribs; but I incline to the supposition that they are sternal ribs, because the inner truncated end of each is in close relation with a bundle of five or six lateral abdominal ossicles, of which the central ossicles in each bundle are nearly straight, while the anterior and posterior describe elliptical curves. If these are really sternal ribs, they are very different, in form, from those of *Sphenodon*.[1] It is by no means easy to arrive at a clear notion of the nature and arrangement of the abdominal ossicles, which extend over the ventral surface between the sternum and shoulder-girdle in front, and the pelvis behind. In front there is an area covered by ossicles of a V shape, the point of the V being turned forwards. The most anterior two of these are 4–5 millim. broad in the

[1] Dr. Baur has stated that the abdominal ossicles of *Sphenodon* are connected by ligament in pairs with the sternal ribs, but I have not yet been able to satisfy myself of the fact.

middle; but, behind, they become narrower in the middle and taper off to mere threads of bone at their outer and posterior ends. This area of V-shaped ossicles can be traced back for 90 millim., and is fully 120 millim. wide. Between the 15th and 20th vertebræ,, narrow and nearly straight bands of bone appear to extend across the abdominal wall, and either to end in, or be connected with, the lateral ossicles already mentioned. The width of the area occupied by the abdominal ossicles, in this region, is not less than 220 millim. In front of the right pubis there are three broad curved plates, the inner ends of which turn forwards, and which fill up the space between the præpubic process and the position which would be occupied by the epipubic cartilage, if such existed. The posterior abdominal ossicles in Crocodiles are, as is well known, closely connected with the pubis *Sphenodon* requires re-examination in relation to this point.

The sacral vertebræ are, unfortunately, much injured; but the centrum of the first (Plate XXVI. [Plate 27] fig. 10) appears to be amphicœlous, the convex posterior face of the 23rd (or 24th) centrum fitting into it in front, and the convex anterior face of the second sacral fitting into it behind.

The rib of the first sacral vertebra measures 18 millim. transversely, and its expanded outer end 23 millim.

In the form of the articular surfaces of the centra, in the great development of the cervical ribs, and in the absence of intercentral ossifications, the skeleton of the trunk of *Hyperodapedon* departs from *Sphenodon* more widely than in any other particular.

The skull has been completely detached from the matrix, and all its most important characters are beautifully displayed.

Viewed from above (Plate XXVI. [Plate 27] fig. 1), its contour presents the form of a broad-based isosceles triangle. The base, represented by the occipital region, measures 210 millim.; while the distance from the centre of that region to the rounded apex, formed by the conjoined premaxillary bones, is 160 millim. The hinder moiety of the dorsal region of the skull displays the great supratemporal fossæ (*s.t*), which are somewhat rounded (50 millim. wide and 58 millim. long), and are separated by the relatively narrow parietal region of the skull (20 millim. wide), which presents no parietal foramen. In the front moiety, the orbits (*or.*), of a half-oval shape (50 millim. long and 30 millim. wide), are separated by the broad frontal portion of the skull, which is 40 millim. wide. In front of these, again, and of the broad and short nasal bones, is the single anterior nasal aperture (*a.n*), which is triangular, with the apex forwards, and is 20 millim. broad by 24 millim. long. In the living animal, this opening would have

been divided into two by the nasal septum ; but, no doubt, this was entirely cartilaginous, and hence, in the fossil, the aperture appears single. Laterally, it is bounded by a strong ascending process of each premaxilla.

In this respect there is a very marked difference between *Hyperodapedon* and *Sphenodon*. In the latter, the median end of each premaxilla sends up a broad and strong process, which, united with its fellow, ascends in front of the nasal septum to the nasal bones, and thus the two nasal apertures become widely separated by bone. Laterally, on the other hand, the premaxillæ are united with the maxillæ by a short process, which has no ascending branch.

In *Hyperodapedon*, as in *Sphenodon*, the median end of the oral face of each premaxilla is elongated downwards into a recurved process (Plate XXVI. [Plate 27] figs. 2, 3, 5, *r.p*); and the two processes, closely applied together by their inner surfaces, form the beak, or rostrum, in which the upper jaw terminates. In *Sphenodon*, these rostral processes are broad and flattened from before backwards. Their broad truncated ends descend but little beyond the dentary edge of the mandible, when the mouth is shut, and present two tooth-like eminences. Moreover, their inner sides, closely applied through the greater part of their length, diverge so as to leave a median notch below. In *Hyperodapedon*, the rostral processes are thick and semi-circular in section, the inner, mutually applied, sides being flat and the outer faces convex. Each tapers to its extremity, and the apices of the two are conjoined to form the sharp conical extremity of the beak. The rostrum, as a whole, is much more curved than in *Sphenodon*, and descends far lower in front of the mandibular symphysis. There is no dentary substance upon any part of the rostrum of *Hyperodapedon*; and the aspect of its external surface leads me to believe that it was coated with a horny sheath.

In *Sphenodon*, the anterior end of the mandible lies altogether behind the broad premaxillary rostrum, when the mouth is shut. In *Hyperodapedon*, on the contrary, the rostrum is received between the rostral processes of the mandible.

The lateral view of the skull (Plate XXVI. [Plate 27] fig. 2) shows that the orbits looked more upwards in *Hyperodapedon* than in *Sphenodon*; the lateral temporal fossæ (*l.t*) are relatively much smaller and have a very peculiar ear-like contour, while the bony boundaries of these parts are much stronger. In *Hyperodapedon*, I can find nothing but bone in the region which should be occupied by the post-temporal fossæ. The contour of the alveolar edge of the maxilla in *Sphenodon* is slightly convex downwards and slightly concave

inwards. In *Hyperodapedon*, the contour is very strongly convex both downwards and inwards, and this feature, combined with the great length and recurvature of the premaxillary rostrum, confers a very peculiar aspect on the skull (see figs. 1 and 3, p. 645).

In the under view of the skull of *Sphenodon* (fig. 6, p. 645), the maxillary and palatal regions present little difference from those of ordinary Lizards. The palatal area slowly widens from before backwards, and its maxillary boundaries are slightly concave inwards. Running parallel with the posterior half of each of these is the dentigerous ridge of the palatal bone, bearing a single series of some seven or eight teeth, which, like those of the maxilla, are acutely conical. Between these and the posterior maxillary teeth is the deep groove into which the mandibular teeth are received. The palatal and maxillary teeth of opposite sides are separated by the widest part of the palatal area, formed by the pterygoid bones in the middle, and the palatals at the sides. The long oval posterior nares are wide and conspicuous, occupying, as they do, the greater part of the space between the anterior end of the palatal series of teeth and the premaxillary rostrum (see fig. 6, p. 645).

In *Hyperodapedon* (Plate XXVI [Plate 27] fig. 3) the alveolar edges of the maxille describe a curve which is strongly convex towards the middle line, and correspondingly concave outwards. Their posterior ends are very far apart, but in the anterior halves of their extent they approach so closely as to leave only a narrow palatal area. At their anterior ends they again slightly diverge. Behind, three longitudinal rows of obtusely conical teeth are set between the groove for the mandible and the outer margin of the maxilla, but only one of these rows is continued forwards along the anterior half of the length of the maxilla (see fig. 4, p. 645).

The space included between the mandibular groove and the curved posterior boundary of so much of the dentigerous area of the palatal bones as is left visible in the specimen by the dislocated mandible is occupied on each side by four rows of obtusely conical teeth, which take a direction roughly parallel with one another and with the series of maxillary teeth. Only one of these series of teeth is continued forward alongside of the single part of the series of maxillary teeth.

The palatal bones are undistinguishably united, either with the pterygoids, or over them, in the anterior narrow part of the palate, which ends in a semilunar margin, concave forward. The space between this and the posterior face of the root of the premaxillary beak is, for the most part, filled by a broad plate of bone which

represents the vomers. The posterior nares must have been very small, but, on the left side, between a concave edge of this vomerine plate on the inner side, the premaxilla, in front, and the maxilla, externally, there is a small aperture, which I take to be the posterior nasal opening (Plate XXVI. [Plate 27] fig. 3, *p.n*). The articular condyles of the quadrate bones are elongated from side to side, and present cylindroidal surfaces. They lie about 25 millim. behind a vertical line drawn from the occiput, when the roof of the skull is horizontal.

In *Sphenodon* (see fig. 3, p. 645) the rami of the mandible appear nearly straight in the greater part of their length, both in the lateral and the ventral aspects. In the latter, their anterior ends present a sudden incurvature towards the symphysis, which is not longer than in ordinary Lizards; and, as in them, the union of the rami is effected by ligament. The contours of the alveolar edges of the rami have an upward concavity, which is so slight as to be hardly perceptible; and, viewed from above, they form a narrow arch with nearly straight sides. The inner and superior angle of the symphysial end of each ramus is separated by an interspace from its fellow, above the symphysis. The surface of the ramus at this part is tooth-like in aspect, from the density of the bone of which it is composed. Externally, just where the bent portion of the ramus passes into the straight part, there is a strong conical tooth, the base of which is embedded in the substance of the ramus. This is followed by a series of distinct, acutely conical teeth (also ankylosed to the jaw); these increase in size backwards up to the last three, which gradually diminish. The anterior six or seven of these teeth are very close set, but quite separate.

In *Hyperodapedon*, the mandibular rami are extremely massive, and are ankylosed together in front, throughout their long symphysis (Plate XXVI. [Plate 27] fig. 4). The anterior and superior angle of each is prolonged into a "rostral" process (*r.m*), which passes upwards, outwards, and forwards. The two thus leave a wide V-shaped interval, into which the end of the premaxillary beak is received when the mouth is shut. These mandibular rostral processes were probably clothed, like the premaxillary rostrum, with horn; and, with the interlocking premaxillary beak, must have constituted a pair of pincers of great strength. Behind this forked mandibular beak, the upper contour of each ramus is strongly concave upwards, in correspondence with the maxillo-palatal convexity, and its close-set teeth are worn to a sharp scissor-edge, which fitted into the fore part of the mandibular groove of the upper jaw. Throughout the symphysial region, the two rami lie close together and form a parallel-

Fig. 1.—Skull of *Hyperodapedon*, side view.

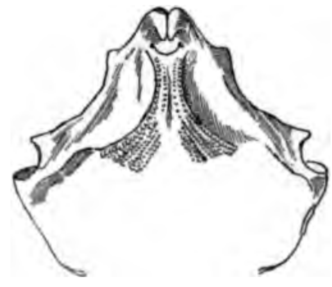


Fig. 4.—Skull of *Hyperodapedon*, under view.

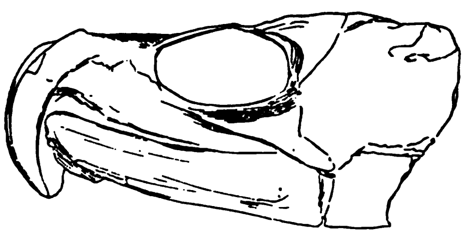


Fig. 2.—Incomplete Skull of *Rhynchosaurus*, side view.

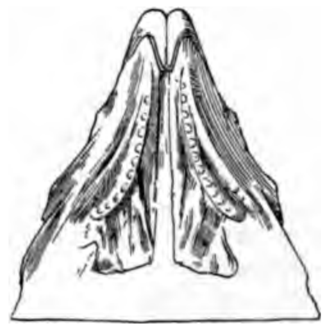


Fig. 5.—Skull of *Rhynchosaurus*, under view.

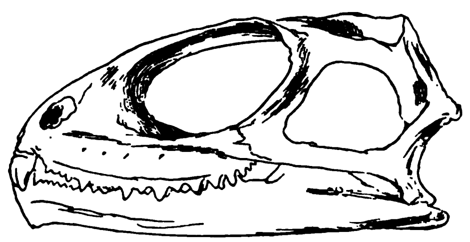


Fig. 3.—Skull of *Sphenodon*, side view.

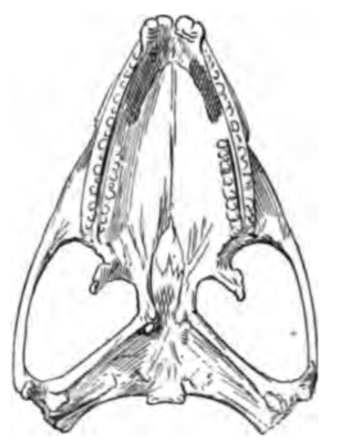


Fig. 6.—Skull of *Sphenodon*, under view.

FIGS. 1-6.—*Diagrammatic views of the Skulls of* Hyperodapedon, Rhyncho aurus, *and* Sphenodon, *illustrating the variations in their proportions and form.*

sided body of the width of the fore part of the palate; but, behind, the rami diverge, sweep outwards in a curve which corresponds, at first, with that of the mandibular groove in the broad part of the palate, and then pass to their articulation with the quadrate. The angle of the ramus appears to have extended considerably behind this articulation, but its exact length and shape cannot be determined.

The alveolar edges of the rami begin to show teeth rather behind the middle of the symphysis, and the series of teeth extends for 60 millim. behind this point. In the front part of the series, the teeth are so close-set as to form a palisade-like continuous ridge, worn upon the two faces to a sharp edge. There are about 6 teeth in a length of 10 millim., and each tooth is 5 millim. high, but at about 7 millim. from the hinder end of the series the teeth become separate. Here they present rounded summits, and their outer surfaces are convex and unworn (Plate XXVI. [Plate 27] fig. 6).

Measurements of parts of the Skull of Hyperodapedon *in millimetres.*

Nasal aperture, 27 long by 24 broad at the base.	
Orbit, 48 long, 35 wide.	
Narrowest part of interorbital region, 40.	
Supratemporal fossa ...	50 long, 45 wide.
Parietal region	20 wide.
Lateral temporal fossa .	23 wide, 41 in perpendicular depth.
Premaxillary rostrum .	25 thick at the base from before backwards.
„ „	30 broad from side to side.
„ „	35 in a straight line from base to apex.
Extreme width of dentigerous area	93
„ length „ „	82
Width of alveolar face of posterior end of maxilla	14
„ „ „ „ palatal	24
Diameter of the bases of teeth	3 to 4
Length of symphysis of mandible	56
Breadth of middle of symphysis of mandible at narrowest between the anterior parts of the dentary edges	23
Depth of the rami at this part	30
Length of each half of the mandibular rostrum from base	20
Greatest depth of ramus from the dentary edge to the lower border	45
Total length of ramus, probably	190
Posterior nares	6 wide by 4 long.

Dr. Woodward has afforded me the opportunity of examining a very instructive, though fragmentary, specimen of the fore part of the skull of a large *Hyperodapedon*, the property of Mr. Grant of Lossiemouth. The premaxillary rostrum is nearly entire and in connexion with the facial bones, as far as the anterior boundary of the orbit on

the left side. The anterior end of the left ramus of the mandible, with its rostral process nearly entire, is almost in place (fig. 7), and on the opposite side of the matrix there is the almost complete impression of the right mandibular rostral process (fig. 8). Moreover, a cast of the outer surface of the left rostral process of the premaxilla is preserved in one of the halves of the matrix. The left rostral process itself is quite free, and can be lifted out and examined on all sides. Including the anterior extremity, of which only the impression remains, it is 57 millim. long, 23 millim. deep, and 13 millim. thick at its proximal end. The anterior face is more strongly curved than the posterior, and somewhat flattened, and it is rather obtusely pointed at its free end. The inner face is flat, and was evidently closely applied

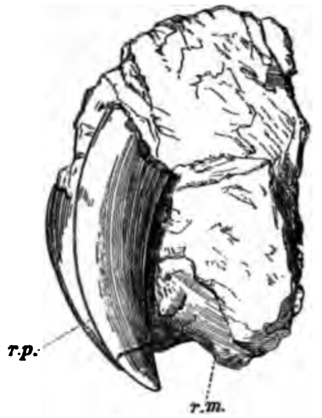


FIG. 7.—*Hyperodapedon Gordoni.* Mr. Grant's specimen. Left side.

FIG. 8.—*Hyperoaapedon Gordoni.* Mr. Grant's specimen. Right side.

to that of the opposite rostral process in the greater part of its extent; but, in the course of fossilization, a thin layer of matrix has been interposed between the two. About the posterior third, the inner face of each rostral process slopes sharply outwards, and the upper margin becomes rounded as it bounds the external nares. Both the inner and the outer surfaces of the bony substance of the rostral processes are marked by fine close-set longitudinal grooves, and the surfaces of the rostral processes of the mandible present similar markings.

The convex face of the left premaxillary rostral process fits closely into the concavity of the cast, to which I have referred, and presents fine longitudinal ridges which answer to the grooves on the surface of the bone. I conclude, therefore, that the soft parts and any horny sheath that may have existed must have decomposed and

left the bone bare before the sandy matrix set round the imbedded skeleton.

Of the bones which enter into the composition of the shoulder-girdle of *Hyperodapedon*, the specimen presents remains of the interclavicle and the clavicle, the coracoid, and the scapula. The interclavicle is a long narrow bone, thin and spatulate towards its posterior end. The anterior end bends somewhat sharply towards the dorsal side; but the shape of its extremity, and whether it was provided with transversely elongated lateral processes or not, cannot be ascertained. On the left side it is in connexion with a strong and long curved bone, which is obviously a clavicle. Nothing more than the edge of a bone which I take to be the scapula can be seen, but the left coracoid is well preserved. It is a cheese-cutter-shaped bone, with a broad blade and a comparatively narrow neck, which widens out again to the glenoidal extremity,

In *Sphenodon*, the anterior end of the interclavicle is not bent upwards, and is produced into two strong transverse arms, with which the clavicles are articulated. The scapula and the coracoid very early became undistinguishably united; while, in *Hyperodapedon* they appear to have remained, as usual, separate.

The principal bones of the left fore limb are seen nearly in their natural relations (Plate XXVI. [Plate 27] fig. 11).

The humerus has a widely expanded proximal end of a rhomboidal shape. In the middle, the shaft is rounded for a short distance, and then expands into the broad and thick distal end, the ventral face of which presents a deep intercondyloid fossa. On the inner side there are indications of a "median" canal. The ulna is stout, with a prismatic olecranar prominence, and is somewhat curved longitudinally so as to be concave to the interosseous space. The radius is more slender and nearly straight.

The structure of the carpus is not recognizable. The five metacarpals are preserved in various conditions of completeness. The most remarkable feature about them is that they do not seem to have differed to any notable extent in length (17 millim.); but while the first, second, and third are proportionally very broad (about 10 millim.), the fourth has a width of not more than 7 millim., and the fifth of 5 millim.

The humerus, radius, and ulna in *Sphenodon*, though more slender, are very similar; but the ulna is longer in proportion to the radius; the first metacarpal is considerably shorter and at the same time thicker than the second, while the second and fourth are a little shorter than the third, and the fifth is about as long as the first; and all

have much slenderer proportions than those of *Hyperodapedon*. The fore foot of the extinct Lizard must in fact have been remarkably short and thick in its proportions.

Measurements of the Shoulder-girdle and Fore Limb in millimetres.

	Hyperodapedon.	*Sphenodon.*
Interclavicle, length	90 (about)	31
„ greatest width	17	3
Clavicle	100 (about)	20
Coracoid, length	58	
„ breadth	42	11
Humerus, length	130	33
„ width at proximal end	62	11
„ „ at distal end	?	11
„ shaft in the middle	20	2·5
Radius, length	74	20
„ width, proximal	20	4
„ „ distal	13	4
Ulna, length	74	25
„ width, proximal	30	5
„ „ distal	20	5
Metacarpals :—		
i.	...	6·5
ii.	...	9·5
iii.	17	11·0
iv.	...	10·0
v.	...	6·0

The right half of the pelvis is exposed: but the pelvic bones are a good deal crushed, and it is difficult to arrive at an unquestionable interpretation of the appearances they present. There is no doubt, however, as to the position of the obturator foramen, bounded in front by the pubis and behind by the ischium. The former bone (Plate XXVI. [Plate 27] fig. 12, *pb*) is transversely elongated, and somewhat narrow in the middle; it widens out at both ends. At the inner extremity it is flat and thin, and presents a convex symphysial contour. At the outer extremity it is developed forwards into a strong prepubic process and backwards into a thick acetabular portion. The bone is therefore quite Lacertilian. The thick acetabular portion of the ischium (Plate XXVI. [Plate 27] fig. 12, *is*) is in connexion with that of the pubis, and the concave obturator margin of the bone can be well made out. The difficulty is to say how much of the mass of bone which lies behind this point (*x*, fig. 12) belongs to the ischium and how much to the ilium, which seems to be crushed down upon

the ischium. If, as appears probable, the posterior contour of the ischium is indicated by the curved depression (*a a*, fig. 12), the ventral half of the pelvis will be quite like that of ordinary Lizards, and the rest of the bony matter belongs to the ilium. On the other hand, the form of the ischium in *Rhynchosaurus* rather leads to the supposition that the ischium was expanded inwardly and prolonged further backward, so as to be unlike that of *Sphenodon*.

The chief bones of the right hind limb (Plate XXVI. [Plate 27] fig. 12) are fairly well seen. The femur is directed forwards, outwards, and dorsad, its proximal end being close to the acetabulum. The bones of the leg are sharply bent at the knee, where they lie close to the distal end of the femur, but slightly dislocated backwards. At their distal ends they are in close proximity to the remains of the tarsus and metatarsus. The femur is a short and stout bone, bent so as to be slightly concave on the ventral and convex on the dorsal surface. The proximal end is a good deal injured, but it obviously expanded to its articular surface and was quite Lizard-like. The middle of the shaft is rounded and little more than half the diameter of the ends of the bone. The inner condyle is stouter than the outer, and between the two there is a deep intercondyloid depression. At about the junction of the middle with the proximal third, the ventral face exhibits a longitudinal elevation, which I take to be the commencement of a strong trochanteric ridge such as exists in *Sphenodon*. The tibia and fibula are not fully exposed, but the former must have been much shorter than the femur; the distal end is trihedral; the middle of the shaft is flattened, and the proximal end somewhat expanded. The fibula seems to have had a similar form, but it was much more slender. Only fragments of the tarsal bones are preserved.

There are indications of five metatarsals, only three of which are represented in (Plate XXVI. [Plate 27] fig. 12). They increase in length from the first to the third, if not to the fourth. The first is 17 millim. long, the second 35 millim., the third 45 millim., and each has a breadth of about 10 millim. Of the fourth only an imperfect impression of the proximal half remains. These four metatarsals lie close together and parallel with one another. The fifth digit was set at a distance from the fourth, as is usual in Lizards, but only the impression of the characteristically broad basal end of the fifth metatarsal is preserved.[1] The first phalanx of the first digit is 14

[1] The indications of the structure of the metatarsus, which I have interpreted as above, are somewhat obscure. Even with large-sized figures, their value could hardly be estimated without examination of the original.

millim. long, and the second seems to have had about the same length. There are two fragmentary phalanges of the second and third digits respectively.

Measurements of the Pelvis and Hind Limb.

	Hyperodapedon.	*Sphenodon.*
Pubis from acetabulum to medial edge	74	19
Femur, length	121	40
„ breadth, proximal end	41	8
„ „ middle	23	3
„ „ distal end	36	8·5
Tibia, length	80	26
Fibula, length	80 (about)	25·5
Metatarsal i.	17	8
„ ii.	35	12·5
„ iii.	45	15

It is obvious, even from these imperfect data, that the hind foot of *Hyperodapedon* was longer than the fore foot, though shorter in proportion than that of *Sphenodon*. It seems also in the gradation of the digits to have departed less from the ordinary Lacertilian foot than the fore foot does.

The comparison of all parts of the skeleton, which has now been made, leaves no doubt as to the close relations between *Hyperodapedon* and *Sphenodon*. At the same time it makes clear the existence of a number of differences, of which the following appear to me to be the most important:—

1. The centra of the præsacral vertebræ are ossified throughout and more or less opisthocœlous, especially in the cervical region. Moreover there are no intercentral ossifications.

2. The anterior cervical vertebræ have long and strong ribs.

3. The external nares are not separated by bone.

4. The conjoined premaxillary processes form a long, conical, curved, pointed rostrum, which is received between two rostral processes of the mandible. All these were devoid of teeth, and probably ensheathed in horn.

5. The palatal area is very narrow in front and wide behind, with strongly curved lateral boundaries.

6. The posterior maxillary and palatal teeth are multiserial.

7. The rami of the mandible are united in a long symphysis behind which they diverge widely, and their dentigerous edges are strongly concave upwards as well as outwards.

8. The mandibular teeth are set into a close, apparently continuous palisade in front, and they become distinct and conical only at the posterior end of each series.

9. The fore foot is remarkably short and stout, with metacarpals of equal length. I find no evidence of the existence of an "ect-epicondylar foramen" in the humerus.

Rhynchosaurus, although allied to *Hyperodapedon*, is sharply distinguished from the latter by its vertebral and cranial characters; and, in some respects, it occupies an intermediate place between *Hyperodapedon* and *Sphenodon*.

A specimen in the British Museum (to which I shall refer as No. 1) shows the head and trunk in almost undisturbed relation, though much damaged in some parts. The length, from the snout to the sacrum, could not have exceeded 280 millim.; so that the animal was only a little larger than the specimen of *Sphenodon* of which the measurements are given above; and, as the skull was about 80 millim. long, it had about the same proportion to the trunk as in *Sphenodon*.

The centra of the thoraco-lumbar vertebræ are about 10 millim. long and amphicœlous. They present, at each end, a hemispherical concavity, each of which occupies about a fourth of the length of the centrum, the two middle fourths being occupied by bone. No specimen which I have seen shows the characters of the centra of the cervical or sacral vertebræ, nor throws any light upon the question of the existence of anterior cervical ribs. There is no evidence of the occurrence of intercentral ossifications.

The abdominal ossicles, so far as they are visible, resemble those of *Hyperodapedon* and *Sphenodon*, but no specimen I have seen enables their details to be satisfactorily made out.

The skull, in its general characters, resembles that of both *Hyperodapedon* and of *Sphenodon*. In contour, it is intermediate between the two, having the occiput relatively somewhat broader than in *Sphenodon* and much narrower than in *Hyperodapedon*.

The anterior nasal aperture is single, as in *Hyperodapedon*, and the strong recurved premaxillary rostrum has essentially the same structure, and probably was ensheathed in a horny envelope. On the other hand, the dentary edge of the maxilla is but very slightly convex downwards; and, viewed from below, there is a corresponding difference from *Hyperodapedon*. The outward lateral concavity and inward convexity of the dentary edges of the maxillæ are very slight, and consequently there is no such anterior narrowing and posterior

widening of the palatal surface as in *Hyperodapedon*. The palatal bones are not fully exposed in any specimen, but in one there is evidence that they bear certainly not more than two longitudinal rows of teeth, perhaps only a single row; consequently they are narrow, as in *Sphenodon*; and, as in the latter genus, leave the anterior portions of the pterygoid bones, which lie between them, uncovered (Plate XXVII. [Plate 28] fig. 1, *pt*). The symphysis of the mandible is relatively short, and the rami do not curve outwards as they do in *Hyperodapedon*. The mandibular rostral processes, between which the premaxillary rostrum is received, are short and obtuse (see fig. 2, p. 645).

Thus the skull of *Rhynchosaurus* resembles that of *Hyperodapedon* and differs from that of *Sphenodon*, in its single anterior nasal aperture, its premaxillary and mandibular rostral processes, and, perhaps, in possessing more than one series of palatal teeth; but, in general form, and in the shape of the maxillæ, palatal bones, and rami of the mandible, it departs far less from *Sphenodon* than *Hyperodapedon* does. In another respect, *Rhynchosaurus* appears to differ from both *Hyperodapedon* and *Sphenodon*, in that no distinct teeth are discernible on the dentary edges either of the maxillæ or of the mandible. Without microscopic examination of sections of the parts, it is impossible to say whether the maxillæ and the mandible of *Rhynchosaurus* were really edentulous or not. If they were, this genus will present an interesting approximation to the Anomodontia.

Two other specimens (No. 2, and its counterpart, No. 3) display the coracoids (*co*) in place (Plate XXVII. [Plate 28] fig. 3). These bones are broad and expanded, 34 millim. long and 20 millim. wide, and have convex median edges. Close to this edge of the right coracoid (in No. 2) lies the interclavicle (*i.cl.*), 30 millim. long. It is narrow, blade-like, and bent dorsad at its anterior end. Here it expands transversely into two arms, which are short, but are not improbably broken. The clavicles are wanting, unless the part marked *cl.* in fig. 3 represents one.

In the specimen of *Rhynchosaurus* to which I have already referred as No. 1, much of the skeleton of the right fore limb is preserved. The right humerus is 40 millim. long, and has widely expanded proximal and distal ends. The radius has about the same length. There are more or less well-preserved remains of five metacarpals. The first has about half the length of the second, which is about equal to the third.

In the specimen (No. 2) all five digits of the manus are displayed. The fifth metacarpal, which is broad and short, as in *Sphenodon*, and

three or four of the phalanges of the fifth digit are in place (Plate XXVII. [Plate 28] fig. 3). In all respects, this foot is more like that of *Sphenodon* than that of *Hyperodapedon*.

The impressions of the ischia are very well shown in No. 3 (Plate XXVII. [Plate 28] fig. 4, *is*). They are broadly triangular in shape, with the angles rounded off. The symphysial side is 25 millim. long; while, from the symphysis to the acetabulum, transversely, the bone measures 20 millim. In front of the left ischium there is seen, in the place which ought to be occupied by the pubis, the impression of a broad flat plate (Plate XXVII. [Plate 28] fig. 4, *pb*), 25 millim. from side to side by 10 antero-posteriorly, the posterior edge of which is, for its inner two-thirds, in close contact with the front edge. of the ischium, leaving only a small space to represent the obturator foramen. I cannot take this impression to represent anything but the pubis, though its form and position are somewhat unusual. The femur is 57 millim. long, and the shaft is curved like an $\int$. The tibia and fibula are each 50 millim. long. The astragalus and calcaneum are separate (as in *Sphenodon*), and have the ordinary Lacertilian form. A large distal tarsal bone (as in *Sphenodon*) affords an articular surface for the fifth metatarsal, which, with the four phalanges of its digit, is preserved (Plate XXVII. [Plate 28] fig. 4, *v*). This digit differs but little in size and form from the corresponding digit in *Sphenodon*; and it is therefore remarkable that the fourth metatarsal of *Rhynchosaurus* is very much broader than that of *Sphenodon*, and half as long again. The third and second metatarsals are nearly as broad, but shorter. The first is relatively shorter and thicker (Plate XXVII. [Plate 28] fig. 5).

Two imperfect series of tail-vertebræ show that, in the anterior caudal region, the vertebræ were provided with long and strong chevron bones (Plate XXVII. [Plate 28] fig. 2).

The evidence which has now been adduced appears to me to prove that *Hyperodapedon*, *Rhynchosaurus*, and *Sphenodon* constitute a peculiar group of Lacertilia, the skeletons of which are distinguished from those of all other recent or extinct known forms by the combination of the following characters, namely:—the premaxillary rostra; the longitudinal series of palatal teeth, bounding a groove, between which and the maxillary teeth the hinder mandibular teeth are received; the abdominal ossicles; and the absence of procœlous præsacral vertebræ. This group of *Sphenodontina* falls into two amilies, the *Rhynchosauridæ* and the *Sphenodontidæ*.

The *Rhynchosauridæ* have a single external nasal aperture; edentulous premaxillary and mandibular rostra, probably covered with horn, the former received between the latter; sometimes more than one series of palatal teeth; and either amphicœlous, or more or less opisthocœlous, præsacral vertebræ.

This family contains *Hyperodapedon* and *Rhynchosaurus*, readily distinguished by the cranial, vertebral, and dental differences given above.

The *Sphenodontidæ* have divided external nares; a toothed premaxillary rostrum, not horn-covered, nor received between mandibular rostral processes; a single series of palatal teeth; and amphicœlous vertebræ.

It is very interesting to observe that, so early as the Triassic epoch, the group of the Sphenodontina had attained its highest known degree of specialization, *Hyperodapedon* being in all respects a more modified form than *Sphenodon*. It appears a probable conclusion that in the Permian epoch, or earlier, Lacertilia existed which were less different from *Sphenodon* than either *Hyperodapedon* or *Rhynchosaurus*.

I am unable to discover any feature in the organization of either *Hyperodapedon* or *Rhynchosaurus* which supports the supposition, sometimes entertained, that these reptiles departed from the types of structure found among existing Lacertilia in any greater degree than these (*e.g. Monitor*, *Chamæleo*, *Gecko*, *Sphenodon*) do from one another, or that they present any approximation to other Orders of Reptilia.

The evidence now offered concurs with that afforded by the structure of *Telerpeton*, in establishing the belief that the Lacertilian type of organization had, in the Triassic epoch, attained perfectly clear definition from all others; and it further shows that, in *Hyperodapedon*, the type had attained a degree of specialization on a level with that exhibited by any modern Lizard.

The relations of the Sphenodontina with other groups of Reptiles of approximately the same age, in which the anterior ends of the jaws tend to assume the characters of a beak, with or without palatal teeth (*Dicynodon*, *Endothiodon*), and with such forms as *Placodus*, cannot, I think, be profitably dealt with until more is known of the organization of the latter. I may add that I am unable at present to see any good grounds for the approximation of *Simædosaurus* to *Hyperodapedon*.

In his valuable account of the Indian species of *Hyperodapedon* ('Indian Pretertiary Vertebrata,' vol. i., 1885), Mr. Lydekker assigns

various detached bones to this genus on very fair grounds of probability. The absence of intervertebral ossifications in *H. Gordoni*, however, would seem to diminish that probability so far as the vertebræ are concerned.

EXPLANATION OF THE PLATES.

PLATE XXVI. [PLATE 27].—*Hyperodapedon Gordoni.*

Fig. 1, 2. Upper and lateral views of the skull. ½ nat. size.
3. The palatal surface of the skull, so far as the adherent mandible permits it to be seen. ½ nat. size.
4. Under view of the mandible. ½ nat. size.
5. Front view of the premaxillary rostrum and the anterior nares. ½ nat. size.
6. Series of mandibular teeth : *a*, anterior, *p*, posterior end. Nat. size.
7. The remains of the atlas, and fig. 8, the succeeding cervical vertebræ. Nat. size
9. Præsacral vertebræ, with the proximal end of a rib. Nat. size.
10. The remains of the first sacral vertebra. Nat. size.
11. The left fore limb. ¼ nat. size.
12. The right hind limb. ¼ nat. size.

PLATE XXVII. [PLATE 28].—*Rhynchosaurus articeps.*

Fig. 1. Under view of an imperfect skull. Nat. size.
2. A series of caudal vertebræ. Nat. size.
3. The right shoulder-girdle, ventral aspect (No. 2), and the left fore limb, dorsal aspect (No. 3) Nat. size. It is doubtful whether *cl* is really the clavicle.
4. Impressions of the left pubis and ischium, and remains of the bones of the left hind limb as they lie in No. 3. Nat. size.
5. Right hind foot, ventral aspect (No. 1). Nat. size.

DISCUSSION.

THE PRESIDENT remarked that he felt he only expressed the sentiments of all the Fellows present in welcoming back their past President to the scene of his former triumphs. The type specimen of *Hyperodapedon* was so imperfect that it was marvellous the characters ascribed to the genus required so little modification in consequence of the far more perfect specimen now described.

Mr. HULKE could only re-echo the President's congratulations on the reappearance of Prof. Huxley. He could but admire the clear manner in which this very interesting reptile had been described by him.

Dr. GEIKIE recalled the early controversies about the age of the Elgin Sandstones, and pointed out that no satisfactory stratigraphical solution of the puzzle had yet been found. A line between the beds with Mesozoic Reptilia and those containing *Holoptychius* would never have been drawn but for the extraordinary contrast of the organic remains. By physical characters it was not possible to separate them.

Prof. SEELEY said that caution was necessary in concluding that such types were limited to one system. The Reptiles of South America associated with *Lepidodendron* and *Schizodus*, partly described by Prof. Cope, have close affinity with some from South Africa which are usually regarded as Triassic.

The form of articulation of the vertebræ being merely generic in Amphibia, it is not surprising to find that some reptiles have opisthocœlous vertebræ. Some recent lizards also

Mintern Bros. imp.

[PLATE 28.]

Quart. Journ. Geol. Soc. Vol. XLIII. Pl. XXVI.

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Mintern Bros. imp.

RHYNCHOSAURUS ARTICEPS.

show peculiar forms of the abdominal ribs, as in *Plesiosaurus*, which are present in many Triassic reptiles, though enveloped with matrix, so as to form abdominal rods like those seen in this fossil. In conclusion, he spoke of the satisfaction he experienced in once more hearing Mr. Huxley.

Mr. LYDEKKER noticed the occurrence of *Hyperodapedon* in India associated with *Parasuchus* and *Belodon*; but the associated vertebræ are amphicœlous. The maxillo-palatines appeared perfectly similar, more so than he at first believed; indeed there was scarcely apparent specific difference between those described by him and those of the new Elgin specimen.

Mr. WHITAKER wished to thank Prof. Huxley for the good lesson given by the absence of dogmatism in his paper.

Dr. BAUR inquired as to the development of the parietal foramen.

Prof. HUXLEY said that he could not find a trace of any such foramen in *Hyperodapedon*.

Dr. BAUR said that this showed the specialization of *Hyperodapedon*. *Simœdosaurus* or *Champsosaurus* must have some relation to *Sphenodon*, but it is also a specialized form. He pointed out some vertebral points of similarity between the former and *Sphenodon*.

With regard to the systematic position of *Hyperodapedon* and its allies he would prefer putting them under the Rhynchocephalia apart from Lacertilia as a group equivalent to Ophidia and Mosasauria.

Dr. BLANFORD described the relative position of the *Hyperodapedon*-beds in India, showing that they were, in all probability, later than the *Dicynodon*-beds, and closely allied, if not identical, with the beds containing fishes of Liassic type. He also noticed that *Uromastix*, an agamoid lizard which shows some points of resemblance in dentition to *Hyperodapedon*, is exclusively herbivorous.

Prof. BOYD DAWKINS said that Mr. Charles Moore's examination of the Rhætic strata which overlie the *Hyperodapedon*-beds of Elgin, proved that the latter occupied *the same palæontological horizon* below the Jurassic series as the *Hyperodapedon*-beds of India mentioned by Dr. Blanford.

The PRESIDENT said, the difficulty about the position of the Elgin beds was not so great as was often supposed. In the Old Red-Sandstone quarries fish-remains are by no means rare, but in the extensive quarries whence the reptiles have been procured no fishes are found, and recently the reptiliferous beds have been shown to overlie unconformably the Holoptychian beds. The whole of the strata are greatly faulted and covered with drift. *Hyperodapedon* and *Dicynodon* certainly occurred together, and the specimens of the latter were being worked out by Dr. Traquair. The Rhætic fossils obtained by Mr. Charles Moore were from a boulder.

Prof. HUXLEY, in reply, said he remembered the time when palæontological papers were not received with such general consent. He begged leave to thank the President and Fellows for the very cordial reception they had given him. He was unable to agree with Dr. Baur's views as to the classification of lizards and their allies, and considered that it was undesirable to multiply great groups too much. The Rhynchocephalian forms did not appear to him to have any real affinity with *Simœdosaurus*, nor were they so much generalized as, for instance, *Telerpeton*. Probably in Carboniferous times the gap between Labyrinthodonts and Lizards was bridged over, and intermediate forms occurred.

XXXVIII

OWEN'S POSITION IN THE HISTORY OF ANATOMICAL SCIENCE

"The Life of Richard Owen," by the Rev. Richard Owen, M.A., 1894 (John Murray), vol. ii., pp. 273–332.

THE attempt to form a just conception of the value of work done in any department of human knowledge, and of its significance as an indication of the intellectual and moral qualities of which it was the product, is an undertaking which must always be beset with difficulties, and may easily end in making the limitations of the appraiser more obvious than the true worth of that which he appraises. For the judgment of a contemporary is liable to be obscured by intellectual incompatibilities and warped by personal antagonisms; while the critic of a later generation, though he may escape the influence of these sources of error, is often ignorant, or forgetful of, the conditions under which the labours of his predecessors have been carried on. He is prone to lose sight of the fact that without their clearing of the ground and rough-hewing of the foundation-stones, the stately edifice of later builders could not have been erected.

In view of these considerations, it was not altogether with a light heart that I assented to the proposal Sir Richard Owen's biographer did me the honour to make, that I should furnish him with a critical estimate of the extensive and varied labours in the field of natural science carried on, for some sixty years, with singular energy, by that eminent man. For I have to reckon, more than most, with those causes of imperfect or distorted vision to which, as I have said, the eyes of contemporaries are obnoxious; and, however confident of the will to correct their effects, I can hardly hope to be entirely successful, without more good fortune than I have a right to look for.

It is an enhancement of the difficulties of the task set me, that what I have to say must be addressed not to experts, but to the general public, to the great majority of whom anatomy is as much a sealed book as the higher mathematics. Even if some few have penetrated a little way, their progress has probably been arrested by the discovery that discussions about anatomical topics are, as a rule, pre-eminently dry and technical. It must be admitted that there is some justification for the popular distaste for anatomical science. The associations of the subject are not wholly pleasing; and, undoubtedly, a long and weary process of initiation is indispensable to the neophyte, who aspires to become an adept and to feel at home in the arcana of the higher anatomy. But I think it ought to be possible to lead any one, who will give a reasonable amount of attention, to a point, from which he may obtain a sufficiently accurate general view of the scope of anatomical science, by a shorter and easier road. In any case, it is laid upon me to attempt to show the way there, inasmuch as the purport of much of Sir Richard Owen's work cannot be understood, nor can his position in science be properly appreciated, unless such a point of view is attained. And in proffering such guide's service it may be well to remind those who accept the offer, that in this, as in so many other cases, 'the longest way round is the shortest way home;' there is nothing for it but to follow the path of history and eschew short cuts, however tempting they may be.

Etymologically, the word 'Anatomy' signifies no more than 'cutting up,' or 'dissection;' but, in course of time, the idea of the chief means by which the structure of animals and of plants was ascertained merged with that of the results it yielded. And since structure, or inward form, is practically inseparable from shape, or outward form, the latter also fell within the range of the anatomist. Further, it was natural enough that the 'function' or use of the parts, the inward and outward form of which they described, should also be treated of by the early and mediæval anatomists; but, as the subject grew, division of labour not only became practically necessary, but was theoretically indicated by the diverse characters of its moieties. Form can be considered without any reference to function; and function can be studied with very little reference to form. One need know nothing of the structure of the eye, for example, to make sure that it is the organ of vision; and a minimum of anatomical lore suffices to establish the familiar truths that the stomach is largely concerned in digestion, and the lungs in respiration. Moreover, the

preliminary training required for the effectual prosecution and advancement of the several studies of form and of function is so different, that, in modern times, the two have steadily tended to fall into different hands. The doctrine of form, whether in the shape of anatomy, histology, embryology, taxonomy (that is, systematic arrangement), or distribution, has become the business of the 'morphologist,' to whom it is a matter of no essential importance whether the subjects of his inquiries are alive or have been dead for millions of years. On the other hand, since functions are the modes of manifestation of the activities of living matter in ultimate resort they must be studied in living beings. The exact forms which the mechanisms of the functions may assume is a matter of subordinate interest. By a curious and somewhat unfortunate chance, the name of 'physiologist,' originally applied to those primal philosophers of ancient Greece who took all Nature for their province, has been inherited by the investigators of function, to whom it has no more special application than to any other students of Nature.

Arrived at the parting of the ways,[1] the one of which leads to the province of physiology, the other to that of morphology, we must take the latter. It is no disparagement to Owen to say that he was not a physiologist in the modern sense of the term. In fact, he had done a large part of his work before modern physiology, in which no progress can be made without clear mechanical, physical, and chemical conceptions, came into existence; and I think it may be doubted whether he ever became fully aware of the vastness of the interval which separates the physiology of John Hunter from the physiology of Johannes Müller and his successors.

Morphology has grown out of anatomy; and anatomy, like most branches of science, if not begotten and born amongst the ancient Greeks, was nurtured and brought up in the way it should go by them. Aristotle, with his immediate predecessors and successors, took the broadest possible view of the subject; the structure of cuttlefishes and crayfishes interested them as much as that of the higher animals. And inasmuch as the taint of impurity which, in ancient times attached to contact with the dead human body, hindered them from obtaining a knowledge of the structure of man directly, they were compelled to divine it, by way of analogy, from their observations on

[1] It will be understood that the separation between Morphology and Physiology can be maintained only so long as the view is confined to the phenomena of form or to those of function. Both are equally important to the aetiologist, who seeks for the causes of biological phenomena.

apes. In fact, their over-confidence in the extent to which the likeness extended led them into serious errors. At the revival of learning, things took another turn. Anatomy sank to the level of a mere handmaid to practical and theoretical medicine. It was only very much later, as the anatomical, like other pure sciences, progressed backwards to their original dignity and independence, that the position of Democritus and of Aristotle was once more reached; and, the study of the living world being taken up for the sake of knowledge alone, man assumed his place as neither more nor less scientifically interesting than his fellows. In the sixteenth and seventeenth centuries, however, the great anatomists of the Low Countries and of Italy had pushed their investigations so far, that more was known of the structure of man than of that of any other animal. It was therefore natural, and indeed unavoidable, that the structure of man should become the standard of comparison, or, in other words, the 'type' to which all other kinds of animal structure were to be referred. The organs of animals were interpreted by the analogy of those of man; the terminology of human structure was extended to the structure of animals in general.

Thus the anatomy of the whole of the rest of the animal world came to be regarded as a sort of annexe of human anatomy; it acquired the name of 'comparative anatomy,' and the conception of the relations of man to the rest of the living world was completely falsified. Man, regarded merely as an animal, was held to be the most perfect of all the works of Nature, below which all the rest could be arranged in a graduated series of forms to the lowest animals; from thence, the descending steps were traced through the vegetable world to the lowest plants; and through the definitely formed to the apparently indefinite mineral constituents of the globe. Hence arose the conception of *une échelle des êtres*, a ladder between stones and men, the rungs of which are the species or kinds of living things.

But gradation implies a certain community between the grades. Degrees of colour are shades of the same colour, or mixtures in which the same colours exist in varying proportions; gradations of form imply similarities of form between the successive steps of the gradation. Thus the idea of a scale of organised beings foreshadows the conception of a more or less widely prevailing unity of organisation among them, and we may regard the promulgation and wide acceptances of Bonnet's doctrine of the 'scale of beings' as the dawn of the higher morphology of modern times.

Though but an imperfect apprehension of a great truth, this

doctrine exerted a highly beneficial influence upon the progress of comparative anatomy. The gradations in structure of the parts and organs of animals were carefully studied. Immense pains were bestowed on the formation of collections of preparations illustrative of gradation ; and there is no more remarkable example of such a collection than that formed by the skill and industry of John Hunter, which was the origin, and still constitutes the nucleus, of the present admirably complete museum of the Royal College of Surgeons of England. A full descriptive catalogue of such a collection must needs be, in itself, an encyclopædia of comparative anatomy. Daubenton, the collaborator of Buffon in France, went to work upon a different, but quite as important, principle. As Buffon opposed the extreme systematizers, who seemed to think it the end of science, not so much to know about an object as to be able to name it and fit it into their system, so Daubenton insisted on the study of each animal as an individual whole. Zoologists who knew and could properly apply every technical term of the *systema naturæ* without the least real acquaintance with animal structure in general, or with that of any single animal in particular, were not to his mind. He occupied himself, therefore, with the production of the series of admirable monographs appended to the descriptions of Buffon in the 'Histoire Naturelle.'[1]

The effect of the co-operation of many zealous workers, along the first of these lines, culminated in the 'Anatomie Comparée' of Cuvier ; while, to the followers of the second method, we owe a host of monographs upon species, or groups of species, belonging to all the divisions of the animal kingdom. In virtue of these labours it came about that, by the year 1830, the province of anatomy had been systematically and, in many regions, minutely surveyed. An adequate, though far from complete, knowledge of all the higher forms had been attained ; and, with the improvement of the microscope, the structural characters of the very lowest forms were beginning to be elucidated.

Thus, the foundations of anatomical science in accurately recorded observations of structure were solidly and securely laid sixty years ago. In fact, the importance of the work done by that time cannot be over-estimated ; for, as Cuvier has somewhere said, whatever may become of hypotheses, the man who has made a permanent addition

[1] It is very much to be regretted that his example has not been more largely followed for the commoner animals. We do not possess, at this moment, a history of even the little group of British Mammals up to the level of the work of Buffon and Daubenton, now nearly a century and a half old.

to our knowledge of facts, has rendered an imperishable service to science. Nevertheless, it is an equally profound truth, of which no one was more conscious than Cuvier himself, that the ascertainment of facts, in the narrowest sense of the word, and the methodical recording of such facts, though it is the beginning of scientific righteousness, is only the beginning. To reach the end, that which is common to groups of details must be carefully sifted out and expressed in general propositions; and these, again, must be tentatively colligated by the guarded and restrained play of the imagination, in the invention of hypotheses, susceptible of verification or negation by further observation.

The vulgar antithesis of fact and theory is founded on a misconception of the nature of scientific theory, which is, or ought to be, no more than the expression of fact in a general form. Whatever goes beyond such expression is hypothesis; and hypotheses are not ends, but means. They should be regarded as instruments by which new lines of inquiry are indicated; or by the aid of which a provisional coherency and intelligibility may be given to seemingly disconnected groups of phenomena. The most useful of servants to the man of science, they are the worst of masters. And when the establishment of the hypothesis becomes the end, and fact is alluded to only so far as it suits the 'Idée,' science has no longer anything to do with the business.

The nature of plants and animals, on the one hand, and of the human mind on the other, is such that the process of generalisation and that of classification, which is the correlative of generalisation, take place instinctively and find expression in common language. The terms 'beasts,' 'birds,' 'fishes,' are the names of certain groups of animals in the popular classification; and, though the user of them may not be able to put his thoughts into words, they imply that he has perceived that the things he calls by these several names have certain common and distinctive characters. And that perception, when it is put into words, is a generalisation, which, in so far as it is accurate, also expresses an empirical 'law of Nature.'

The classifications of the scientific taxonomist are of two kinds. Those of the one sort are merely handy reference catalogues. Such are the 'artificial' systems, useful in their day and for their particular purpose, but of no other value. The others, known as 'natural' classifications, are arrangements of objects according to the sum of their likenesses and unlikenesses, in respect of certain characters; in morphology, therefore, such classifications must have regard only to matters of form, external and internal. And natural classification is

of perennial importance, because the construction of it is the same thing as the accurate generalisation of the facts of form, or the establishment of the empirical laws of the correlation of structure.

To say that deer, oxen, sheep, goats, antelopes, and so on, form a natural group, definable by the co-existence in them of certain forms of bones, teeth, stomach, and the like, which are not co-existent in any other group, is one way of stating certain facts. It is merely another, if we say that it is an empirical law of existing Nature that such and such structures are always found together; and that when we meet with one, there is a *primâ facie* ground for suspecting that the others are associated with it. The finder of a recent skull, provided with a pair of horn-cores, in which the front part of the upper jaw is toothless, may thus safely predict that the animal to which it belonged possessed paired hoofs and a complex stomach, though no amount of merely physiological lore would enable him so much as to guess why the one set of characters is thus constantly associated with the other. The key of the enigma, in fact, does not lie in the hand of the physiologist, but in that of the historian of animal life throughout the ages of its existence.

In the middle of the eighteenth century, the value of the artificial systems invented by Linnæus, as a part of his method of introducing order into the chaos of 'Natural History,' was so much felt, that his clear recognition of their essentially provisional character was ignored by the host of disciples; who, as usual, appreciated most highly, and were most sedulous to imitate, the weakest parts of their master's teachings. The genius of Buffon strove against this tendency to substitute empty schematisms for science almost in vain. Botany became a cataloguing of 'hay;' and zoology, of skins and shells; indeed, of straw, if I may revive a jest of my old friend Edward Forbes—not without serious application even in his time—to the effect that the pure systematic zoologist was unaware that the stuffed skins he named and arranged ever had contained anything but straw.

Before long, however, better days began to dawn; and the light came partly from the purely scientific anatomists, partly from men of more or less anatomical knowledge, in whom the artistic habit of visualising ideas was superadded to that capacity for exact observation which is the foundation of both art and science.

Scientific observation tells us that living birds form a group or class of animals, through which a certain form of skeleton runs; and that this kind of skeleton differs in certain well-defined characters from that of mammals. On the other hand, if any one utterly ignorant of osteology, but endowed with the artistic sense of form, were

set before a bird skeleton and a mammalian skeleton, he would at once see that the two were similar and yet different. Very likely he would be unable to give clear expression to his just sense of the differences and resemblances; perhaps he would make great mistakes in detail if he tried. Nevertheless, he would be able to draw from memory a couple of sketches, in which all the salient points of likeness and unlikeness would be reproduced with sufficient accuracy. The mere osteologist, however accurately he might put the resemblances and differences into words, if he lacked the artistic visualising faculty, might be hopelessly incompetent to perform any such feat; lost in details, it might not even occur to him that it was possible; or, still more probably, the habit of looking for differences might impair the perception of resemblances.

Under these circumstances, the artist might be led to higher and broader views, and thus be more useful to the progress of science than the osteological expert. Not that the former attains the higher truth by a different method; for the way of reaching truth is one and indivisible. Whether he knows it or not, the artist has made a generalisation from two sets of facts, which is perfectly scientific in form; and trustworthy so far as it rests upon the direct perception of similarities and dissimilarities. The only peculiarity of the artistic application of scientific method lies in the artist's power of visualising the result of his mental processes, of embodying the facts of resemblance in a visible 'type,' and of showing the manner in which the differences may be represented as modifications of that type; he does, in fact, instinctively, what an architect, who desires to demonstrate the community of general plan in certain ancient temples, does by the methodical construction of plans, sections and elevations, the comparison of which will furnish him with the 'type' of such temples.

Thus, what I may term the artistic fashion of dealing with anatomy is not only perfectly legitimate, but has been of great utility. The harm of it does not begin until the attempt is made to get more out of this visual projection of thought than it contains; until the origin of the notion of 'type' is forgotten and the speculative philosopher deludes himself with the supposition that the generalisation suggested by fact is an 'Idea' of the Pure Reason, with which fact must, somehow or other, be made to agree.

The old French naturalist Belon, who must have been a good deal of an artist, and illustrated his book, 'L'Histoire de la Nature des Oyseaux,' with many 'naifs portraicts,' initiated this way of dealing with anatomy. The skeleton of a bird is set beside that of a man,

and the reader is left to draw the obvious conclusion as to their 'unity of organisation.' A child may see that skull 'answers' to skull; spinal column to spinal column; ribs to ribs; breast bone to breast bone; wings to arms; and legs to legs, in the two. Later on, Peter Camper, a capital artist as well as an accomplished anatomist, was in the habit of amusing, while he instructed, his class by showing what slight strokes of his chalk sufficed to turn the outline skeleton of a man into that of a dog or of an ox; and how these could be metamorphosed into reptilian or fish forms, without disturbance of their fundamental features.

The cultivator of botany, who went beyond the classification of 'hay,' became familiar with facts of the same order. Indeed, flowering plants fairly thrust morphological ideas upon the observer. Flowers are the primers of the morphologist; those who run may read in them uniformity of type amidst endless diversity, singleness of plan with complex multiplicity of detail. As a musician might say, every natural group of flowering plants is a sort of visible fugue, wandering about a central theme which is never forsaken, however it may momentarily, cease to be apparent.

Vicq d'Azyr, following the line of strict anatomical observation and critical comparison, set forth the correspondences of plan observable in the limbs of the higher vertebrates, and may be considered the founder of the purely scientific higher anatomy.

A few years later, art again took the lead in the person of Goethe. Like all the really great men of literature, Goethe added some of the qualities of the man of science to those of the artist, especially the habit of careful and patient observation of Nature. The great poet was no mere book-learned speculator. His acquaintance with mineralogy, geology, botany, and osteology, the fruit of long and wide studies, would have sufficed to satisfy the requirements of a professoriate in those days, if only he could have pleaded ignorance of everything else. Unfortunately for Goethe's credit with his scientific contemporaries; and, consequently, for the attention attracted by his work, he did not come forward as a man of science until the public had ranged him among the men of literature. And when the little men have thus classified a big man, they consider that the last word has been said about him; it appears to be thought hardly decent on his part if he venture to stray beyond the speciality they have assigned to him. It does not seem to occur to them that a clear intellect is an engine capable of supplying power to all sorts of mental factories; nor to admit that, as Goethe somewhere pathetically remarks, a man may have a right to live for himself as well as for the

public; to follow the line of work that happens to interest him, rather than that which interests them.

On the face of the matter, it is not obvious that the brilliant poet had less chance of doing good service in natural science than the dullest of dissectors and nomenclators. Indeed, as I have endeavoured to indicate, there was considerable reason, a hundred years ago, for thinking that an infusion of the artistic way of looking at things might tend to revivify the somewhat mummified body of technical zoology and botany. Great ideas were floating about; the artistic apprehension was needed to give these airy nothings a local habitation and a name; to convert vague suppositions into definite hypotheses. And I apprehend that it was just this service which Goethe rendered by writing his essays on the intermaxillary bone, on osteology generally, and on the metamorphoses of plants.[1]

I do not think that any one who studies these works, in many ways so remarkable, can doubt that, in the last two decades of the eighteenth century, Goethe arrived, by a generally just, though by no means critical, process of induction, at the leading theses of what were subsequently known as *Naturphilosophie* in Germany, and as *Philosophie anatomique* in France; in other words, that he was the first person to enunciate and conceive as parts of a systematic whole, whatever principles of value are to be met with in the works of Oken, Geoffroy, and Lamarck.

Of the idea of 'unity of organisation' which is fundamental for all three, Geoffroy St. Hilaire himself, writing in 1831, says:

'Elle est présentement acquise au domaine de l'esprit humain; et l'honneur d'un succès aussi mémorable appartient à Goethe.'

Furthermore, the notions of a necessary correlation between excess of development in one direction and diminution in another; of the natural evolution of the animal and vegetable worlds from a common foundation; of the direct influence of varying conditions on the process of evolution, are all to be found, indeed are plainly enunciated, in Goethe's writings. In addition, he sometimes uses

[1] It is an interesting fact that Goethe took up the metamorphosis of plants after he had been led to a conception of the higher vertebrate type; and, also, that he was led to discover the intermaxillary bone in man by deduction from his type-theory. He tells us that, early in the eighties of last century, before the idea of plant-metamorphosis occurred to him, he worked hard at osteology, for the purpose of finding the general type of skeleton, which he conceived must be discoverable 'because the already long accepted comparative anatomy involves the assumption that it exists.' The doctrine current among anatomists at that time, that men are distinguished from apes by the absence of the intermaxillary bone, stood in the way of Goethe's hypothesis; and the importance which he attached to his discovery of evidences of its existence is therefore very intelligible. (See *Osteologie*, 1819, in Goethe's *Werke*, ed. 1867, Bd. 32, p. 191.)

language which may be fairly interpreted as an anticipation of the fundamental teachings of modern histology and embryology; a fact which is by no means wonderful, when we consider that Goethe was well acquainted with Caspar F. Wolff and his writings.

All this is mere justice to Goethe; but, as it is the unpleasant duty of the historian to do justice upon, as well as to, great men, it behoves me to add that the germs, and more than the germs, of the worst faults of later speculative morphologists are no less visible in his writings than their great merits.[1] In the artist-philosopher there was, at best, a good deal more artist than philosopher; and when Goethe ventured into the regions which belong to pure science, this excess of a virtue had all the consequences of a vice. 'Trennen und zählen lag nicht in meiner Natur,'[2] says he; but the mental operations of which 'analysis and numeration' are partial expressions are indispensable for every step of progress beyond happy glimpses, even in morphology; while, in physiology and in physics, failure in the most exact performance of these operations involves sheer disaster, as indeed Goethe was afforded abundant opportunity of learning. Yet he never understood the sharp lessons he received, and put down to malice, or prejudice, the ill-reception of his unfortunate attempts to deal with purely physical problems.

Goethe's contributions to the science of morphology (the very term 'morphology,' in its technical sense, is his) were by no means so widely known to anatomists, or valued by them, as they ought to have been; and it was long before their unquestionable merits were properly appreciated. The most brilliant and, at the same time, the soberest representative of the higher or 'philosophical' anatomy, Geoffroy St. Hilaire, seems, at first, to have known nothing of them. Like Goethe, he had studied mineralogy and botany before taking up anatomy and zoology; an excellent and most industrious observer, he was, at the same time, a man of high intellect and comprehensive views. Intimately associated with young Geoffroy, and only a couple of years older, was Cuvier, one of the most remarkable intelligences of his own or any time. And when these energetic allies turned their attention to vertebrate anatomy, in 1794–5, it was impossible that the facts which had impressed Goethe should fail to lead minds such as theirs towards ideas of the same order. But the minds of the two having a widely different commixture of qualities, the way in which they dealt with the same objective material presented corresponding differences; and these differences went on widening

[1] See, for example, the essay 'Ueber die Spiraltendenz der Vegetation' in the *Morphologie*.

[2] *Morphologie: Geschichte meines botanischen Studiums.*

until, thirty-five years later, these two bosom friends became the antagonists in the most famous of all scientific duels.

However, during the earlier part of his career, I doubt if Cuvier would have categorically denied any of Geoffroy's fundamental theses. And even in his later years, Sir Charles Lyell, many years ago, gave me reasons for the opinion that Cuvier was by no means confident about the fixity of species. There was never any lack of the scientific imagination about the great anatomist; and the charge of indifference to general ideas, sometimes brought against him, is stupidly unjust. But Cuvier was one of those happily endowed persons in whom genius never parts company with common-sense; and whose perception of the importance of sound method is so great that they look at even a truth, hit upon by those who pursue an essentially vicious method, with the sort of feeling with which an honest trader regards the winnings of a gambler. They hold it better to remain poor than obtain riches by the road that, as a rule, leads to ruin.

So far as Cuvier was actuated by such feelings, one can but applaud the course he took. For it is plain to any one, who studies these old controversies by modern lights, that Geoffroy, however good his general ideas may have been, was singularly unfortunate in his attempts to illustrate and enforce them. Even where he was strongest, as upon the topic of the unity of organisation of the Vertebrates, I do not think there is one of his exemplifications of that unity which has withstood criticism; and, in respect of the primary cause of contention in 1830, the comparison of the vertebrate and the cephalopod types, he was quite hopelessly in the wrong.

To any one possessed of Cuvier's vast knowledge and dialectic skill, therefore, it was rarely difficult to cut the ground from under his opponents' feet; to say, in short, whether you are right or wrong, the evidence you adduce in support of your case, where it is not demonstrably contrary to fact, is inadequate. And, in the main, Cuvier has been justified by the larger knowledge of our day. There is no 'unity of organisation' in the sense maintained by Geoffroy, though there is in another sense. Neither Geoffroy, nor Lamarck, adduced any evidence of the modifiability of species sufficient to overcome the strictly scientific arguments adduced on the other side; and it was not till many years later, that the progress of palæontology justified the hypothesis of progressive modification, which Geoffroy himself, fully admitting the lack of evidence, put forward merely as a suggestion.

In later life, however, Cuvier seems to have become so much disgusted by the vagaries of the *Naturphilosophie* school, and to have

been so strongly impressed by the evil which was accruing to science from their example (let those who are disposed to blame him read Oken's 'Physiophilosophy'), that he was provoked into forsaking his former wise and judicious critical attitude; and, in his turn, he advocated hypotheses, which were none the better than those of his opponents because they happened to be in favour with the multitude, instructed and uninstructed. The doctrines of *emboîtement* in embryology; of periodical geological catastrophes; of the fixity of species; of physiological deduction as the basis of palæontology; and the restriction of the scope of biological science to mere observation and classification—which is fairly deducible from some of Cuvier's dicta, though I do not believe he ever intended that it should be—are not one whit more scientifically respectable than the least sober speculations of Geoffroy.

The irony of history is nowhere more apparent than in science. Here we see the men, over whose minds the coming events of the world of biology cast their shadows, doing their best to spoil their case in stating it; while the man who represented sound scientific method is doing his best to stay the inevitable progress of thought and bolster up antiquated traditions. The progress of knowledge, during the last seventy years, enables us to see that neither Geoffroy, nor Cuvier, was altogether right, nor altogether wrong; and that they were meant to hunt in couples instead of pulling against one another. Science has need of servants of very various qualifications; of artistic constructors no less than of men of business; of people to design her palaces and of others to see that the materials are sound and well fitted together; of some to spur investigators and of others to keep their heads cool. The only would-be servants, who are entirely unprofitable, are those who do not take the trouble to interrogate Nature, but imagine vain things about her; and spin, from their inner consciousness, webs, as exquisitely symmetrical as those of the most geometrical of spiders, but, alas! as easily torn to pieces by some unconsidered bluebottle of a fact.

Naturally, it is Cuvier, in his capacity of the man of business, who has been held in almost exclusive veneration by those (and they are always the majority) who engage in merely adding to the capital stock of science. For them, he has done everything and is the highest of exemplars. And justly, for Cuvier's monographs, and the osteological treatises interpolated in the 'Ossemens Fossiles,' are of unsurpassed excellence; while, for the sagacious application of the data of osteology to the interpretation of fossil remains, he has never had a superior. Again, Cuvier's clear logical head and marvellously

wide acquaintance with animal forms enabled him to reform classification; and to set forth, in the 'Règne Animal,' a generalized statement of the facts of animal structure which was, in itself, a sufficient refutation of the doctrine of unity of organisation as it was conceived by Goethe and Geoffroy. The mere quantity of the palæontological work alone which Cuvier turned out is amazing, and it hardly ever falls below the level of the highest excellence. Moreover, Cuvier incidentally did as great service to the cause of sound morphology as any of the philosophical anatomists. He worked out the principles of the latter as far as they could be safely carried, and showed that their method must needs, in the end, stop short for want of a criterion. The study of the connections of parts, by no means always enables us to determine whether they 'answer to one another' or not; and the philosophical anatomists too largely ignored other means of testing their hypotheses.

The constructive efforts of Goethe, with the *Philosophie anatomique* of France and the *Naturphilosophie* of Germany on the one hand, the critical negations of the Cuvierian school on the other, do not represent all the lines of biological work in the period under consideration. There is another, which it is the great defect of Cuvier and his school to have underrated and neglected; while it is the great misfortune of Geoffroy that it made its importance fully felt too late for him. This is Embryology, or Development; that is, the study of the manner in which individual living things acquire the structure which they possess.

The science of development, in the modern acceptation of the term, came into existence when Wolff demonstrated the fallacy of the *emboîtement* theory; and also proved that the leaves, the petals, the stamens, and so forth, of flowering plants do, as a matter of fact, start from one and the same primary form in the bud and become differentiated as they grow. It was thus that, thirty years before Goethe saw how the relations of living forms could be ideally represented, Wolff proved what they in fact are. In quite another sense from that of Goethe's reply to Schiller, the embryologist showed cause for the belief that 'unity of organisation' is not an idea, but a fact. The study of the actual process of individual evolution, thus put on a firm foundation, steadily advanced, until Von Baer[1] arrived at the great generalisation that all such evolution is a progress from relative simplicity to relative complexity; in other words, that it is

[1] My translation of 'Fragments relating to Philosophical Zoology, selected from the Works of K. E. Von Baer,' was published in 'Scientific Memoirs' for February and May 1853. Up to that time, I believe, Von Baer's ideas were hardly known outside Germany.

the gradual differentiation of a relatively homogeneous living substance represented by the egg; that, in so far as all individual living beings start from ova of essentially similar simplicity of structure, and as the earliest steps of their development or evolution are similar, the fundamental unity of their organisation is a fact; on the other hand, that, in so far as the typical forms of the several groups to which they belong are soon assumed, and, thereafter, each pursues the special line of modification characteristic of its group, 'unity of organisation' soon ceases to be strictly predicable. Thus Geoffroy was right about the fundamental unity of animal organisation, and Cuvier was right about the existence of different types irreducible to one another; while each erred in thinking his own views incompatible with those of his opponent.

In the course of the discussions about the corresponding, or answering, parts in different organisms, or in the same organisms, and about questions of classification, a very useful terminology had been invented. When the systematists attempted to construct a scientific classification, they found themselves obliged to discriminate between different kinds of resemblances. Take, for example, the question whether a whale is a fish or not, which, I observe, is not yet quite settled for some people. As a whale is not a little like a fish outside, and lives permanently in the sea, after the manner of a fish, why should it not be classed with the fishes? The answer, of course, is that the moment one compares a whale with any one of the thousands of ordinary fishes the two are seen to differ in almost every particular of structure; and, moreover, in all these points in which the whale differs from the fish it agrees with ordinary mammals. Therefore, zoologists put the whale into the same class as the mammals, not into that of the fishes. But this conclusion implies the assumption that animals should be arranged according to the totality of their resemblances. It means that the likenesses in structure of whales and mammals are greatly more numerous and more close than the likenesses between whales and fishes. The same argumentation applies to the likeness between bats and birds. These are few and superficial, while the resemblances between bats and ordinary mammals are innumerable and profound. Therefore bats go into the class Mammalia, not into the class Aves. In these cases, the estimation of the relative value of resemblances is easy enough; but, in respect of the lesser groups, the problem offered frequently greater difficulties. Even Cuvier, misled by certain superficial resemblances, could refer the acorn-shells and the barnacles to the class of Mollusks.

Thus, in course of time, there arose in the minds of thoughtful systematists a distinction between 'analogies' and 'affinities;' and, in those of the philosophical anatomists, a corresponding discrimination between 'analogous' and 'homologous' structures. Outward resemblances of the character of those which obtain between a whale and a fish, a bat and a bird, were said to be mere analogies, and were properly regarded as of no classificatory importance. The deeper structural likenesses between a whale and a seal, or between a bat and a shrew mouse, on the other hand, were affinities: that is to say, the exhibitors of such resemblances were 'affined' or 'allied' in the sense of belonging to the same classificatory group.[1] So, for the anatomists, the shell of a tortoise and the shell of a crab were merely analogous structures; while the bones of the arm of a man and those of the wing of a bird were homologous.

Homology (ὁμολογία) originally signified agreement either of, or about, things. The word, with its derivatives and allies, such as 'homonymous,' passed into Latin, French, and German; and Anglicised forms of them are to be found in Nathan Bailey's 'Dictionary,' now a century and a half old. Even in its present sense, as an anatomical term, homology was well known as far back as the early years of this century. Owen, writing in 1846, insists upon the fact that, in using the word, he follows established precedent:—

'But, in thus illustrating the term *homology*, I have always felt and stated that I was merely making known the meaning of a term introduced into comparative anatomy long ago, and habitually used in the writings of the philosophical anatomists of Germany and France. Geoffroy St. Hilaire also, in defining the term, acknowledges its source: "Les organes sont *homologues* comme s'exprimerait la philosophie allemande; c'est-à-dire, qu'ils sont analogues dans leur mode de développement," &c. ("Annales des Sciences," tome vi. 1825, p. 341.)'[2]

The last words of the citation from Geoffroy St. Hilaire have a curious significance. Goethe had pointed out, and neither he, nor Geoffroy, nor Oken, were blind to the fact, that the study of development must have a good deal to say about the problems of philosophical anatomy; though, as I have mentioned, that branch of

[1] It is interesting to observe how readily the term 'affinity,' which ordinarily implies blood-relationship, was adopted by those who most strongly repudiated the doctrine of descent.

[2] 'On the Structural Relations of Organised Beings' (*Philosophical Magazine*, xxvii. p. 526).

morphology had not advanced far enough to enable Geoffroy to appreciate its full importance, before the publication of Von Baer's works, in the course of the decade 1828 to 1838. But embryology began to show its capacity for playing the part of a criterion in morphology pretty early. It has already been stated that Wolff demonstrated the homology of leaves, stamens, and carpels, by tracing their development. Later, it was readily shown that Vicq d'Azyr's doctrine of the homology of the limbs had its proof in the observation that they arise from rudiments of similar character and relations. In all the higher vertebrate animals, the fore and hind limbs are, at first, very similar, and they become differentiated by successive steps. So the earliest rudiments of the spinal column, and the manner in which it becomes segmented, are alike throughout.

On the other hand, a favourite speculation of the philosophical anatomists, that the lower jaw is formed by the coalescence of a pair of limbs, for which comparative anatomy seemed to offer some support; and Geoffroy's tempting suggestion that the opercular bones of fishes answer to the ear-bones of mammals, were at once negatived by the study of the development of the parts. Again, the hypothesis that the skull consists of modified vertebræ, advocated by Goethe and Oken, and the subject of many elaborate works, was so little reconcilable with the mode of its development that, as early as 1842, Vogt threw well-founded doubts upon it. 'All efforts to interpret the skull in this way,' said he, 'are vain.'

The preceding sketch of the history of anatomical science, though drawn only in broad outline, may suffice to indicate the courses which naturally suggested themselves to any one taking up the subject in the beginning of the fourth decade of the present century.

There was the brilliant example of Cuvier in the 'Anatomie Comparée,' the 'Mémoires sur les Mollusques,' and the 'Ossemens Fossiles,' for any one disposed to devote himself to the increase of the capital stock of knowledge by museum work, or by anatomical and palæontological monography; there was the path of philosophical anatomy, opened up by Vicq d'Azyr, Goethe, Geoffroy St. Hilaire, Oken, and followed out in the elaborate works of Spix and Carus on the skeleton, with results acutely checked and criticised by Cuvier; there was the study of individual development in its dawn, but with its great future already clearly indicated by Von Baer; there was the question of the development of animals and plants in general, or what is now commonly understood by the term evolution, waiting to be rescued from the region of speculation, to which it had

been relegated for want of positive evidence one way or the other, and a good deal more damaged by its supporters than by its opponents.

It was at this time, namely in 1830, that Owen turned from practical medicine to natural science; and threw himself into the first-mentioned of these paths of exploration, with an energy which reminds one of Geoffroy and Cuvier, when, a little younger, they set out on their remarkable careers. Owen's first recorded publication is an account of an aneurism. The second work in which he engaged was a catalogue of specimens in the museum of the Royal College of Surgeons. But, in the next year (1831), no fewer than eight papers on the anatomy of various mammals, birds, and reptiles which had died in the Zoological Gardens bear his name. This was a pretty good start for a young man of twenty-six to make; but the harvest of the year 1832 bettered that of its predecessor. For without any other work, Owen's time might, one would think, have been fully occupied by the famous 'Memoir on the Pearly Nautilus,' which was published in 1832 and placed its author, at a bound, in the front rank of anatomical monographers. There is nothing better in the 'Mémoires sur les Mollusques,' I would even venture to say nothing so good, were it not that Owen had Cuvier's great work for a model; certainly, in the sixty years that have elapsed since the publication of this remarkable monograph, it has not been excelled; and that is a good deal to say with Müller's 'Myxinoid Fishes' for a competitor.

During more than half a century, Owen's industry remained unabated: and whether we consider the quantity, or the quality, of the work done, or the wide range of his labours I doubt if, in the long annals of anatomy, more is to be placed to the credit of any single worker.

The preparation of the five volumes of the descriptive catalogue of the Hunterian Museum and of the annual courses of lectures demanded from the Hunterian Professor, took Owen over the length and breadth of the animal kingdom and involved the making of special investigations in almost all its provinces. The wide knowledge thus accumulated was eventually summed up and published, first in the lectures on the Invertebrates (1843) and, secondly, in those on the Vertebrates (1860-1868).

As methodically arranged and comprehensive repertories of the anatomy of animals, it may be a question whether these works are equal to the contemporary 'Handbuch' of Siebold and Stannius; but it may quite safely be said of them, that they are based on the results

of a greater amount of personal investigation than any work of the kind except, perhaps, Cuvier's 'Leçons;' and I put the exception doubtfully, inasmuch as Cuvier was aided by highly skilled assistants.

Further, I think that Owen's monographic work occupies a unique position, if one considers, not merely its general high standard of excellence, but the way in which so many of these memoirs have opened up new regions of investigation. I mention the following, as some of the most important from this point of view, in addition to that on the Pearly Nautilus, to which I have already referred.

To begin with the higher animals, Owen's early memoirs on the anatomy of the anthropoid Apes contained by far the most complete and adequate account of their structure, and of the resemblances and differences between them and man, then extant; and they formed the foundation of all subsequent researches in that field. The same may be said of his investigations on the Monotremes and Marsupials, the substance of which is, for the most part, incorporated in the well-known articles of the 'Cyclopædia of Anatomy and Physiology.' These remained, for many years, indeed are still, in most respects, the best source of information about these animals.

The researches on the minute structure and the development of the teeth, summed up in the 'Odontography' (1840-45), and the article 'Odontology,'[1] so far as they deal with the outward form, the microscopic appearances, and the order of succession of the teeth, and furnish a foundation for a useful and consistent nomenclature of dental arrangements, have been of very great service both to the ordinary zoologist and to the student of fossil remains.

In regard to the class of birds, the memoirs on the Apteryx, the Great Auk, and the Dodo are particularly noteworthy; and the article 'Aves' in the 'Cyclopædia of Anatomy and Physiology' very long held its own, as the best summary of avian structure.

The paper on 'Lepidosiren' left no doubt of the piscine affinities of that animal.

Among the Invertebrates we have the article 'Cephalopoda' (1836), the 'Memoir on Limulus' (1873), the 'Researches on the Brachiopoda' (1833), and the description of the terrible parasite of man, *Trichina spiralis*.

In regard to Taxonomy, Owen made a variety of proposals, the consideration of most of which would involve discussions altogether out of place in this sketch. But there is a notable exception

[1] *Encyclopædia Britannica*, 1858.

in the case of the 'attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes' appended to the 'description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *H. bovinus*)' (1848), as to the high value of which I think all zoologists are agreed.

In 1837, Owen, without any pause in the long and important series of anatomical investigations which have been mentioned, began those contributions to palæontology which, in after years, perhaps contributed most to his fame with the public. His first work in this department is a memoir, published in the second volume of the Proceedings of the Geological Society, on an extinct mammal discovered in South America by Darwin in 1833, which Owen named *Toxodon Platensis*. It is worthy of notice that, in the title of this memoir, there follow, after the name of the species, the words 'referable by its dentition to the Rodentia, but with affinities to the Pachydermata and the herbivorous Cetacea;' indicating the importance in the mind of the writer of the fact that, like Cuvier's *Anoplotherium* and *Palæotherium*, *Toxodon* occupied a position between groups which, in existing nature, are now widely separated. The existence of one more extinct 'intercalary' type was established.

From another point of view, this maiden essay in palæontology possesses great interest.

It is with reference to Owen's report upon the remains of Toxodon that Darwin remarks in his journal, six years later: 'How wonderfully are the different orders, at the present time so well separated, blended together in different points of the structure of the Toxodon!' while, in his pocket-book for 1837, he records: 'In July opened first notebook on Transmutation of Species. Had been greatly struck from about the month of previous March on character of South American fossils, and species on Galapagos Archipelago. These facts (especially latter) origin of all my views.'[1]

Unless it be in the 'Ossemens Fossiles,' I do not know where one is to look for contributions to palæontology more varied, more numerous, and, on the whole, more accurate, than those which Owen poured forth in rapid succession between 1837 and 1888. Yet there was no lack of strong contemporaries at work in the same field. De Blainville's 'Ostéographie;' Louis Agassiz's monumental work on fossil fishes, achieved under the pressure of great obstacles and full of brilliant suggestions; Von Meyer's long series of wonderfully accurate memoirs, with their admirable illustrations executed by his own hands, all belong to Owen's generation. But, perhaps, the

[1] *Life and Letters*, vol. i. p. 276.

fairest comparison is with Cuvier; and I do not think that those who have had to concern themselves with these subjects will rank any of Cuvier's memoirs higher than those of Owen on *Mylodon*, *Megatherium*, *Glyptodon*, *Macrauchenia*, and other extinct South American animals, which followed up the account of *Toxodon*.

In 1838 appeared the memoir on the Stonefield Slate mammals, then the oldest known, pointing out their marsupial affinities, and with this the later investigations on the Purbeck mammals may be grouped. In 1839–40, we have the first indication of the wingless birds of New Zealand, widening out, in after years, into the long series of memoirs on *Dinornis* and the like. In 1841, the description of the triassic Labyrinthodonts of Central England, which, with Von Meyer's earlier and later work, was the commencement of the elucidation of the triassic fauna in all quarters of the world, made its appearance. In 1844, Owen published the memoir on Belemnites, which had a distinct value, though not perhaps quite that assigned to it at the time. In 1845, followed the first view of the wonderful extinct faunæ of South Africa and Australia, so largely extended by Owen himself in later years. In 1849, the first of the long series of memoirs on British fossil reptiles appeared; in 1863, the description of the famous reptilian bird Archæopteryx.

It is a splendid record; enough, and more than enough, to justify the high place in the scientific world which Owen so long occupied. If I mistake not, the historian of comparative anatomy and of palæontology will always assign to Owen a place next to, and hardly lower than that of Cuvier, who was practically the creator of those sciences in their modern shape; and whose works must always remain models of excellence in their kind. It was not uncommon to hear our countryman called 'the British Cuvier,' and so far, in my judgment, the collocation was justified, high as the praise it implies.

But when we consider Owen's contributions to 'philosophical anatomy,' I think the epithet ceases to be appropriate. For there can be no question that he was deeply influenced by, and inclined towards, those speculations of Oken and Geoffroy St. Hilaire, of which Cuvier was the declared antagonist and often the bitter critic.

That Owen was strongly attracted by the *Naturphilosophie* of Germany is evidenced, not merely by his attitude towards the problems of philosophical anatomy, but by his article on Oken in the 'Encyclopædia Britannica;' and by the fact that the translation of Oken's 'Lehrbuch der Naturphilosophie'[1] was undertaken at his

[1] *Physiophilosophy*, translated by Tulk. Ray Society, 1847.

instance. Thus, when Owen passes from matters of anatomical fact and their immediate interpretation to morphological speculation, it is not surprising that he also passes from the camp of Cuvier into that of his adversaries.

In the advertisement of the work 'On the Archetype and Homologies of the Vertebrate Skeleton,' published in 1848, Owen says:—

'The subject of the following essay has occupied a portion of my attention from the period when, after having made a certain progress in comparative anatomy, the evidence of a greater conformity to type, especially in the bones of the head of the vertebrate animals, than the immortal Cuvier had been willing to admit began to enforce a reconsideration of his conclusions, to which I had previously yielded implicit assent.'

In fact, what I may call 'Okenism' colours Owen's whole cast of thought on these matters, and his admiration for Oken finds frequent vent in his writings. Thus, in a note at p. 8 of the 'Archetype and Homologies of the Vertebrate Skeleton' (1848), we find:—

'Oken's famous "Programm ueber die Bedeutung der Schädelknochen" was published in the same year (1807) as Geoffroy's memoir on the Bird's Skull; but it is devoted less to the determination of "special" than of "general homologies;" it has, in fact, a much higher aim than the contemporary publication of the French anatomist, in which we seek in vain for any glimpse of those higher relations of the bones of the skull, the discovery of which has conferred immortality on the name of Oken.[1]

And the 'Conclusion' of the same work (pp. 171–172) abounds in the sense of the Okenian philosophy. The explanation of the facts of morphology is sought in the 'principle of vegetative repetition;' in the interaction of a 'general and all-pervading polarising force,' with an adaptive or special organising force,' identified with the Platonic ἰδέα. Whether they be sound or unsound, nothing can be more opposed to the Cuvierian tradition than speculations of this order.

The 'Programm' to which these sympathetic references are made, opens with some sentences which are worth attention, since they furnish a typical example of the speculative procedure of the *Naturphilosophie* school.

'A vesicle ossifies, and it is a vertebra. A vesicle elongates into a tube, becomes jointed, ossifies, and it is a vertebral column. The tube gives off (according to laws) blind lateral canals; they ossify, and it is a trunk skeleton. This skeleton repeats itself at the two

[1] There are even stronger expressions to the same effect in the French version of the treatise, *Principes d'Ostéologie comparée*, published in 1855.

poles, each pole repeats itself in the other, and they are head and pelvis. The skeleton is only a developed, ramified, repeated vertebra; and a vertebra is the pre-formed germ of the skeleton. The entire man is only a vertebra.'

All this may be in accordance with the 'Idée,' and demonstrable *a priori*; but the plain, prosaic inquirer into objective truth may be excused if he finds nothing in it but a series of metaphorical mystifications; for which, so far as they are to be taken seriously, no empirical justification ever existed. There is not, and there never was, any ground for believing that a vertebra is an ossified vesicle; or that a vertebral column, or a trunk skeleton, is produced in the way asserted; or that a head is a repeated pelvis, or *vice versâ*; while the intelligibility of the final assertion that 'the entire man is only a vertebra,' is not apparent. The spirit which animates these oracular utterances pervades all the writings of Oken and his school; it provided Cuvier with the subject-matter of his severest, as well as of his most justifiable sarcasms; and every one who has the interests of sound science at heart must feel Cuvier's debtor for the pertinacity with which he combated, and finally drove out of the field of science, this pseudo-philosophical word-play.

I do not for a moment suggest, indeed I cannot imagine, that Owen approved of such extravagances as those which I have cited; but that he was deeply influenced by the philosophy of Oken, bringing it, apparently, in his own mind into harmony with that of the English Platonists, and especially of Cudworth, is a conclusion which can hardly be avoided. The following passages alone appear to me to be decisive:—

'Now, besides the ἰδέα, organizing principle, vital property, or force, which produces the diversity of form belonging to living bodies of the same materials, which diversity cannot be explained by any known properties of matter, there appears also to be in counter-operation, during the building-up of such bodies, the polarizing force pervading all space, and to the operation of which force, or mode of force, the similarity of forms, the repetition of parts, the signs of the unity of organisation may be mainly ascribed.

'The Platonic ἰδέα, or specific organising principle or force, would seem to be in antagonism with the general polarizing force, and to subdue and mould it in subserviency to the exigencies of the resulting specific form.' [1]

'Now, however, the recognition of an ideal Exemplar for the

[1] *On the Archetype and Homologies of the Vertebrate Skeleton* (1848), p. 172.

Vertebrated animals proves that the knowledge of such a being as Man must have existed before Man appeared. For the Divine mind which planned the Archetype also foreknew all its modifications.

'The Archetypal idea was manifested in the flesh, under divers such modifications, upon this planet, long prior to the existence of those animal species that actually exemplify it.

'To what natural laws or secondary causes the orderly succession and progression of such organic phenomena may have been committed we are yet ignorant. But if, without derogation of the Divine power, we may conceive the existence of such ministers, and personify them by the term "Nature," we learn from the past history of our globe that she has advanced with slow and stately steps, guided by the archetypal light, amidst the wreck of worlds, from the first embodiment of the Vertebrate idea under its old Ichthyic vestment, until it became arrayed in the glorious garb of the Human form.'[1]

Those who know Owen's mind only on the side reflected in the exact observations, the clear-headed and sagacious interpretations, of the anatomical and palæontological memoirs, should ponder over these and other passages of like tenor, if they wish to form a just judgment about the position which he took up in morphology; and, later, in regard to the Darwinian revivification of the doctrine of evolution. On the speculative side, the very same mind has a distinct leaning towards realistic mysticism, while remaining liberally, perhaps prodigally, eclectic. A sublimated Theism, after the manner of Cudworth, lies at the foundation of Owen's speculations; while the 'Archetype' takes the position of a Platonic ἰδέα, indeed, almost that of an Alexandrian λόγος. The essentially naturalistic abstractions—'secondary causes,' 'forces,' and 'polarity'—are personified and regarded as agents.

If, in the 'Nature of Limbs' (pp. 84, 85), the argument from Design is momentarily shattered by the admission that some parts of animals are 'made in vain;' it is immediately redintegrated by the suggestion that they are illustrations of the design manifested in the 'Archetype.' The looking to 'natural laws' and 'secondary causes' for the 'progression' of organic phenomena' is the substantial acceptance of evolution, as set forth by Goethe, Oken, Lamarck, and Geoffroy; but the picture of 'Nature,' advancing 'amidst the wreck of worlds,' fits in, no less admirably, with the catastrophism of Cuvier.

Owen's morphological labours appear to me to be completely pervaded by the spirit, and restricted to the methods, of the philosophical anatomists; if I may, for the nonce, use that name in a

[1] *On the Nature of Limbs*, pp. 85, 86. 1849.

limited sense, for the scholars of Oken, rather than for those of Geoffroy. But, from this point of view, the theory of the vertebrate skeleton had been so elaborately worked out by Spix (1815), Carus (1828), and others, that the vein might well seem to be exhausted. Carus, especially, had visualized his hypotheses in diagrams, to which he gave the names of 'Grundform' and 'Schema;' and which are the equivalents of the 'Archetype' and its derivatives. Thus, when Owen took up the subject, many years after Carus, there really was nothing new in principle to be done, so long as the method of his predecessors was followed. All that could be hoped from renewed investigation, along the same lines, was the rectification of erroneous, and the suggestion of unsuspected, homologies. And this is what we find; new homologies for the cranial bones; original speculations respecting the nature of the bony walls of the inferior cavities of the skull; as to the proper connections and homology of the pectoral arch; and so on.

I believe I am right in saying that hardly any of these speculations and determinations have stood the test of investigation, or, indeed, that any of them were ever widely accepted. I am not sure that any one but the historian of anatomical science is ever likely to recur to them; and considering Owen's great capacity, extensive learning, and tireless industry, that seems a singular result of years of strenuous labour.

But it will cease to be so remarkable to those who reflect that the ablest of us is a child of his time, profiting by one set of its influences, limited by another. It was Owen's limitation that he occupied himself with speculations about the 'Archetype' some time before the work of the embryologists began to be appreciated in this country. It had not yet come to be understood that, after the publication of the investigations of Rathke, Reichert, Remak, Vogt, and others, the *venue* of the great cause of the morphology of the skeleton was removed from the court of comparative anatomy to that of embryology.[1] When developmental investigation had proved that even the segmentation of the vertebrate body is not its primary condition; that such segmentation without founding it largely on embryology cannot be traced throughout the cranial region; that a process of chondrification, or formation of cartilaginous hard-parts, precedes ossification, and is not the same in the skull as in the spinal column; that bones

[1] And even this appeal is not final. We have still to look to palæontology for confirmation or contradiction of our deductions from the facts of embryology. Biological evolution is based on the history of life on our planet, as evidenced by the facts of palæontology, however these facts may be supplemented and speculatively interpreted.

are not all similar in respect of their mode of origin; it was obvious that no satisfactory theory of the skeleton could be attained without taking these facts into serious consideration, and, indeed, without founding it largely on embryology.

It would be a great mistake, however, to conclude that Owen's labours in the field of morphology were lost, because they have yielded little fruit of the kind he looked for. On the contrary, they not only did a great deal of good by awakening attention to the higher problems of morphology in this country; but they were of much service in clarifying and improving anatomical nomenclature, especially in respect of the vertebral region.

Apart from questions of classification, the only special work of Owen which deals directly with the greater problems of biology, is the discourse on 'Parthenogenesis, or the Successive Production of Procreating Individuals from a single Ovum,' originally delivered in the form of the opening two lectures of the Hunterian Course for 1849.

In these discourses, an attempt is made to correlate, and furnish an explanation of, the phenomena of sexless proliferation; that is to say, of the production of offspring by a plant or an animal, without the intervention of sex. In the vegetable world, such phenomena, as exemplified by the growth and detachment of buds or bulbs, or of young plants, like those formed on strawberry 'runners,' have been known from time immemorial; among animals, they were first carefully elucidated by Trembley and Bonnet in the middle of the eighteenth century.

One of the commonest and most striking cases is that of the plant lice, or *Aphides*, which are the commonest of pests in our gardens. The young, which these animals produce with such wonderful fertility in summer, are all fatherless. So are the drones in a hive of bees.

Among the aphides, this state of things, as a rule, persists throughout the summer; and it is not until the autumn arrives that the broods produced take on the characters of males and females, which die after their functions are performed and the eggs are laid. The eggs remain dormant during the winter; and when they hatch, in spring, the aphides produced are sexless, though in some respects they resemble the true females. These sexless forms produce living broods, having the same characters as their producer; and these give rise to others, in like manner, through the summer. It has been proved that this state of things may be maintained for three years, by keeping the insects warm and supplied with food; indeed, there is no positive evidence that it need ever come to an end.

The males and females are, in many respects, different from the sexless proliferators. Thus, to superficial observation, it appears as if the sexed 'generation,' which may be called the form A, was succeeded by a certain number of sexless 'generations' of the form B; these by A, these by B again, and so on. In other words, the 'generations' A and B alternate.

In the course of the early decades of the nineteenth century, the wide extension of exact investigation among the lower groups of the animal kingdom, especially the polypes, worms, star-fishes, ascidians, crustacea, and insects, brought to light a great number of new facts of the same order; and, in 1842, the Danish zoologist, Steenstrup, collected all of them known at that time, and applied to the phenomena the general formula of the 'Alternation of Generations.' He was met, at the outset, by a difficulty of nomenclature. In the majority of cases, the one term, or the one set of terms, of the alternation is sexless. The germs from which its offspring are produced are not true eggs and are uninfluenced by males. Therefore, it is obviously inexact to call these proliferating forms 'females.' Steenstrup got over the difficulty by terming them 'nurses;' though, thereby, he undoubtedly somewhat strained the usually admitted attributes of a nurse. I do not imagine that Steenstrup supposed that he had contributed anything towards the explanation of these remarkable phenomena by the nomenclature he proposed. However this may be, his work was of much use by drawing the attention of biologists to their general nature, no less than by bringing into one view all the various forms of proliferation which are exhibited by living matter, and all the physical and metaphysical difficulties, with which the problem of animal and vegetable individuality bristles. Objections might be raised to the term 'Parthenogenesis,' used by Owen, not merely for the autonomous proliferation of true females, but for the production of progeny by organisms which are not really female, and the vestalship of which is therefore physically indefeasible. In fact, it is strictly applicable only to a comparatively few cases among insects and crustacea. And even here, the queen-bee, under ordinary circumstances, would have to be excluded. The fatherless drones are, usually, not merely produced by a true female; but she is already mother, in the ordinary sense, of thousands of daughters.

But questions of names are of no particular importance. We know what the processes denoted by the term 'Parthenogenesis' are; and the point is to ascertain how far Owen's work contributed to a better knowledge of them; or to that construction of an explanation of the phenomena which is the end of investigation.

With respect to the first point, the work on 'Parthenogenesis' contains no addition, that I am aware of, to the common stock of observed facts. In truth, the great majority of the subjects of these processes are either the smaller insects and crustacea, which lay out of Owen's range of study; or the marine invertebrates, which were, in those days, hardly accessible to any but persons who lived on, or by, the sea. Moreover, the investigation lay eminently in the province of the histological microscopist, in which Owen was less at home than elsewhere.

In trying to form a judgment of the value of the explanation offered, it is a necessary preliminary to consider what there was to explain.

Among the animals with which we are familiar, proliferation, or the production of offspring, invariably implies the concurrence of two parents, a father and a mother. We are, therefore, naturally led to regard this method of proliferation as the rule, and any other as an exception. But, as we have seen, if our daily experience had been derived from many of the lower animals and plants, we might just as well have been led to think sexless proliferation the rule, and the other the exception. Whatever the outward form of the process of proliferation, in substance it always comes to the same thing. It is the detachment of a parcel, A, of the living substance of the parent, which either before, or after, detachment evolves into a complete, physiologically independent, organism. There are innumerable cases in which this process takes place, in virtue of the autonomous activities of the living substance of an organism. The progeny in this case is a detached fragment of A, and nothing else. Why is it that, in equally numerous other cases, a parcel of the same kind may be similarly detached from A, but does not evolve, unless another parcel, B, of living substance, derived from the same, or another, organism, not merely comes into contact with A, but fuses with it; so that the substance of the progeny is A+B, and not merely A? What we want to explain is, not only why sexless proliferation takes place in the animals or plants in which it occurs, but why it does not take place in other closely allied forms. It is not legitimate to assume that sexless proliferation is secondary and exceptional; and sexual proliferation primary and normal. On the face of the matter, it is just as likely to be the other way.

In the essay under consideration, however, Owen starts with this assumption. He conceives that B is the agent by which a certain 'spermatic force' is transmitted to A; and that, when apparently sexless proliferation takes place, the evolution of the germs is really due to the presence in them of this hypothetical 'spermatic force,'

transmitted from the first sexual proliferation. Starting from the established truth that, where sex is concerned, the essential step of the production of progeny is the coalescence of substances contained in two cells, one derived from the one parent, and one from the other, and the subsequent division and subdivision (with concomitant growth) of the combined mass into the primary cells of which the embryo is constructed, Owen goes on to say (p. 5):—

'Not all the progeny of the primary impregnated germ-cell are required for the formation of the body in all animals; certain of the derivative germ-cells may remain unchanged, and become included in that body, which has been composed of their metamorphosed and diversely combined or confluent brethren; so included, any derivative germ-cell, or the nucleus of such, may commence and repeat the same processes of growth by imbibition, and of propagation by spontaneous fission, as those to which itself owed its origin; followed by metamorphoses and combinations of the germ masses so produced which concur to the development of another individual; and this may be, or may not be, like that individual in which the secondary germ-cell or germ-mass was included.'

Again (p. 72):—

'It would be needless to multiply the illustrations of the essential condition of these phenomena. That condition is, the retention of certain of the progeny of the primary impregnated germ-cell, or, in other words, of the germ-mass, unchanged in the body of the first individual developed from that germ-mass, with so much of the spermatic force inherited by the retained germ-cells from the parent cell or germ-vesicle as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them.

'How the retained spermatic force operates in the formation of a new germ-mass from a secondary, tertiary, or quaternary derivative germ-cell or nucleus, I do not profess to explain; neither is it known how it operates in developing the primary germ-mass from the impregnated germ-vesicle of the ovum. In both we witness centres of repulsion and attraction antagonising to produce a definite result.'

But the primary assumption that this 'spermatic force' is necessary to the evolution of germs, that, therefore, sexless proliferation is only, as it were, sexual proliferation, one or more degrees removed, begs the whole question, which is exactly whether spermatic influence is, or is not, necessary to proliferation.

The other part of Owen's hypothesis, that proliferation depends upon the presence, in the proliferating region, of unchanged de-

scendants of the primitive spermatized cells of the embryo, could not and cannot be supported by observation; and is, indeed, contradicted by plain facts. In mosses, for example, there are very few parts of the whole organism which will not, under favourable circumstances, give rise to bud-like germs, whence new mosses proceed. And, in closely allied animals, in which the cells of the respective ovaries are equally near in descent to those of the embryo, the one will regularly proliferate, without male influence, and the other will never do so.

Owen, in fact, got no further towards the solution of this wonderful and difficult problem than Morren and others had done before him. But it is an interesting circumstance that the leading idea of 'Parthenogenesis;' namely, that sexless proliferation is, in some way, dependent upon the presence, in the prolifying region, of relatively unaltered descendants of the primary impregnated embryo cell (A + B)—is at the bottom of most of the attempts which have recently been made to deal with the question. The theory of the continuity of germ-plasm of Weismann, for example, is practically the same as Owen's, if we omit from the latter the notion that the endowment with 'spermatic force' is the indispensable condition of proliferation. The great progress of knowledge, about these matters, since 1849, lies in the demonstration of the importance of a certain formed material which is met with in the nuclei of cells; of the fact that this substance, growing and dividing, is distributed from the nucleus of the primary cell to the nuclei of all the cells of the organism; that, in sexual proliferation, the nuclear substances of A and B pass, bodily, into the nucleus of the resulting embryo cell, without losing their independence, and are similarly transmitted to all the cells of the adult; whence it follows that every histological element of the adult living body thus produced contains associated, but yet materially distinct, descendants of the nuclear elements derived from each parent.

This discovery ranks, in my judgment, as the greatest achievement of morphological science since the establishment of the cell theory.[1] Its importance as a factor in every theory of heredity is obvious; and it must have an equally important influence upon all theories of proliferation. But, for the present, I must express the opinion that it affords very little more help towards a scientific explanation of the phenomena of 'Parthenogenesis' than Owen's theory afforded in the infancy of histological inquiry. Except by the help of assumptions, of which there is no proof, I do not see that

[1] I refer to the morphological generalisations known by this name: not to any hypotheses based upon them.

modern speculation, at present, gives us any better explanation why the leaves of some plants prolify readily and regularly, while those of others never do so; or why female cockroaches never exhibit sexless proliferation while queen-bees always do so. The ingenuity which fits hypotheses to facts by the help of other hypotheses is always worthy of admiration; but, if it is to be useful, its purely speculative character should never be lost sight of. If science is to retain its strength, it must keep in touch with the solid ground of observation. In reading some of the biological literature of the present day, I sometimes rub my eyes and wonder whether I am not dreaming of the good old days of the *Naturphilosophie*.

In the preceding pages I have endeavoured to give the general reader an outline sketch of the scope and the course of modern biological science; of the condition of its several great divisions when Sir R. Owen commenced his career sixty-four years ago; of the influence of his work upon the extraordinarily rapid advance of biology in the course of that time; and it may be well that, arrived at the end of my task, I recall my allusion, at the outset, to the special difficulties in the way of the satisfactory performance of it.

It does not appear to me that anything need be said here about the many scientific controversies in which Owen was engaged. I should be of this opinion if I had not been concerned in any of them; for I do not see what good is to result from the revival of the memory of such conflicts. And whether I am right or wrong in this opinion, I am well assured that, if anything is to be said upon this topic, I am not the proper person to say it.

But notwithstanding my determination to ignore controversies, and a strong desire to appreciate rather than to criticise, I am sensible that the discussion of the 'Archetype' and of 'Parthenogenesis' not merely allows the wide differences of opinion, which unhappily obtained between Sir R. Owen and myself, to appear, but occupies an amount of space which may be thought excessive, in relation to that filled by my endeavour to do justice to the great and solid achievements in Comparative Anatomy and Palæontology which I have recounted.

But this really lay in the nature of things. Obvious as are the merits of Owen's anatomical and palæontological work to every expert, it is necessary to be an expert to discern them; and endless pages of analysis of his memoirs would not have made the general reader any wiser than he was at first. On the other hand, the nature of the broad problems of the 'Archetype' and of 'Parthenogenesis'